INHERITANCE OF RESISTANCE TO *Phytophthora infestans* (Mont.) de Bary IN HYBRID DERIVATIVES OF *Solanum demissum* Lindl.

A Thesis

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DOCTOR OF SCIENCE

by

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INTRODUCTION.

The existence in Mexico of wild species of potato resistant to Phytophthora infestans has been known for many years. The possibility of breeding hybrids from them possessing blight resistant qualities was demonstrated at Cambridge in 1909 by Salaman when he found that a selfed progeny of S. edinense contained plants which remained free from the disease under blight producing conditions (Salaman 1949). About the same time Dr. J.H. Wilson, working at St. Andrews, made crosses with the blight resistant species S. demissum and continued breeding to improve the economic qualities of the selections. Salaman, satisfied that resistance was attainable, proceeded to collect wild species of the genus, including S. demissum, and to embark on a breeding programme based on interspecific hybridisation designed so as to combine the quality of resistance of the wild types with the agronomic qualities of domestic varieties. By 1926 this work had produced a collection of seedlings bred from S. demissum which were endowed with reasonably good economic characteristics and were unaffected by blight. This material served to indicate that blight resistance and high yielding capacity may be present together in one variety (Salaman 1929).

Research on similar lines was commenced in Germany by /

by Broili in 1912 and in 1923 the material was taken over by K.O. Muller who continued the research work thereafter. In the U.S.A. the search for resistant varieties was also actively pursued, but at first the investigations were mainly concerned with field resistance as observed in commercial varieties of S. tuberosum such as Ekishirazu (Reddick 1923). Later, S. demissum was employed as the source of resistance qualities.

When the work to be reported here was started in 1932, comparatively little was known about the inheritance of resistance to the disease and no variety suitable for commercial purposes had been produced. Also, nothing was known about specialisation in Phytophthora infestans although later in that year the first observations on this phenomenon were made. Then blight appeared on certain seedlings which had previously been unaffected by the disease, both in Britain (O'Connor 1933) and in Germany (Schick 1932, Muller 1932), and the prospects of defeating the disease consequently receded. This apparent breakdown in resistance was found to be due, not to any change in the host plant, but to the appearance of new specialised strains of the fungus.

The work to be discussed here was designed as a systematic attempt to produce varieties resistant to Phytophthora and also suitable for commercial purposes. The initial material comprised cultures of wild species and species hybrids of unknown genetic constitution. These in the first instance were subjected to test with a culture of P. infestans collected from /

from the field in Scotland and borne by commercial varieties of potato. It soon became apparent that the relationships between host and parasite were complex and that a satisfactory understanding of the problem must await the separation of the hereditary units for resistance in the plant and the development of specialisation in the pathogen. In view of these circumstances it will be appreciated that the data obtained in the earlier generations were difficult to interpret. For the present purposes it is proposed to depart from the chronological sequence of the experiments and to discuss in the first place the relationships between the resistance of plants of known genetic constitution and the specialised strains of the parasite that have become established over the last twenty years.

Much of the data contained in the following pages have been published (Black 1943, 1945, 1949, 1950, 1952). Copies of these are attached.

MATERIALS AND METHODS.

The plants and seedling progenies employed for test purposes were derived from four main breeding systems, viz.:

(1) Multiple Hybrid. - The earlier generations were produced by the late Dr. Wilson, St. Andrews, who made the initial crosses over forty years ago (Fig. 1). The writer received seedling W800(2) for breeding purposes, but as far as he is aware no critical tests for resistance to blight were made in any of the preceding generations.

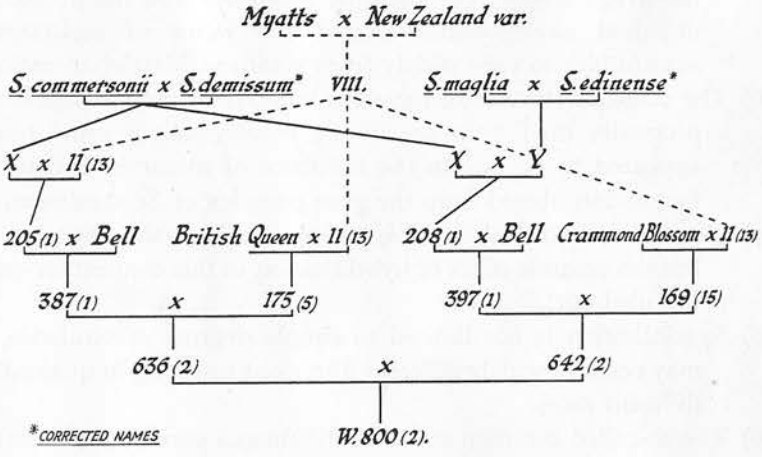

FIG. 1.

The variety of S. demissum employed by Dr. Wilson cannot be identified with certainty, but it is probable, in view of the limited material available at the time, that it was the same as that employed by the writer in the remaining three schemes of breeding. This variety is now included in the Commonwealth Potato Collection under the reference CPC 2127.

(2) S. demissum-S. tuberosum Hybrids. - The original cross of this material was made in 1932 using variety CPC 2127 of /

of S. demissum. The family tree is shown in Fig. 2. The early generations showed irregularities in chromosome behaviour. Seedling 877a(34), however, appeared to be normal and was widely employed as a parent.

(3) S. Rybinii-S. demissum-S. tuberosum Hybrids. - The original cross was made in 1937 from S. Rybinii CPC 1311 and S. demissum CPC 2127. Chromosome behaviour was regular throughout (Thomas, 1945), due to the initial synthesising of a blight-resistant tetraploid from the diploid S. Rybinii and the hexaploid S. demissum. This material (Fig. 3) proved highly satisfactory for genetical work.

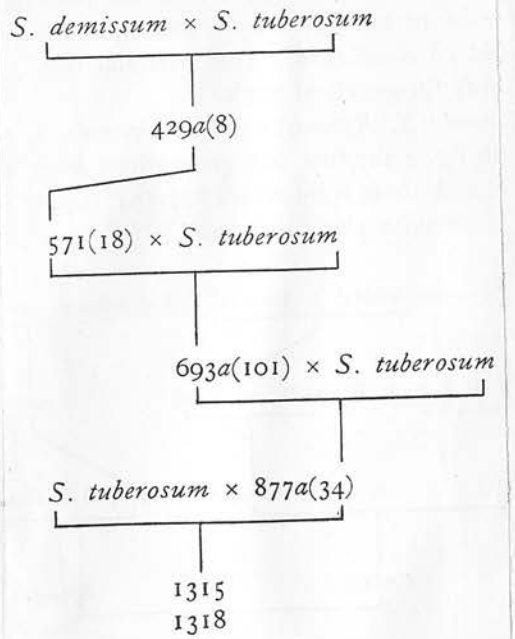

FIG. 2.

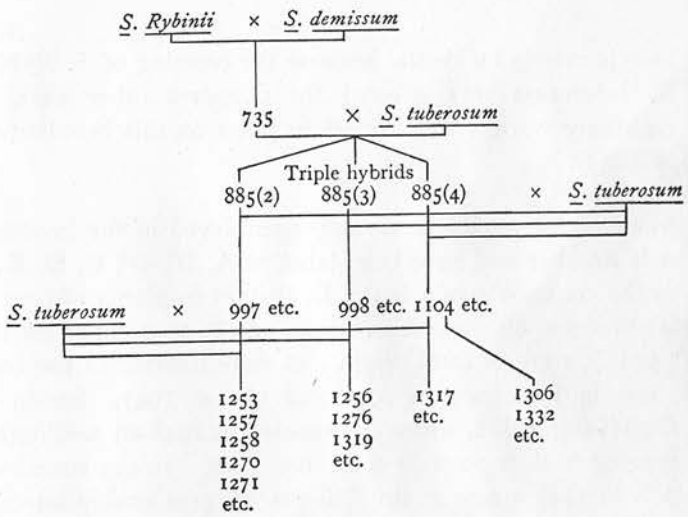

FIG. 3.

(4) (S. tuberosum x S. Rybinii) x (S. demissum x S. tuberosum). As shown in Fig. 4 the first two generations from S. demissum are identical with those from which 877a(34) (Fig. 2) was bred. This pedigree includes also S. Rybinii (CPC 1311), but its presence here is merely incidental because the crossing of S. Rybinii and S. tuberosum was effected for purposes other than blight-resistance work. The important plant on this breeding scheme is 882(5).

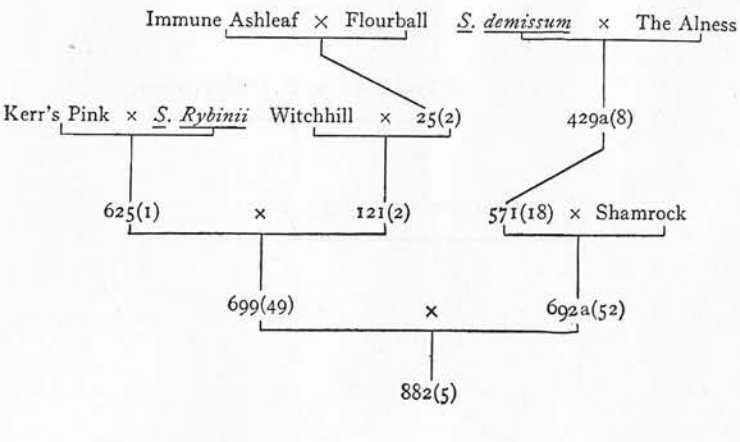

FIG. 4.

The ten strains of Phytophthora infestans employed in the experiments to be described are as follows:-

Strain A. The common strain found in commercial crops of S. tuberosum.

Strain B^1. Isolated in 1939 from the field trial plots.

Strain B^2. Isolated in 1944 in the course of experiments and probably arose from Strain B^1.

Strain C. Isolated in 1947 from the field trial plots.

Strain D. Isolated in 1947 from the field trial plots.

Strain /

Strain E. Isolated in 1948 from experimental plots of seedlings undergoing trial in Tanganyika and obtained through the courtesy of Dr. G.B. Wallace.

Strain F. Isolated in 1949 in the course of experiments with strain E from which it probably arose.

Strain G. Isolated in 1951 from experimental plots of seedlings undergoing trial in Kenya and obtained through the courtesy of Dr. R.M. Nattrass.

Strain H. Isolated in 1951 from experimental plots of seedlings undergoing trial in Kenya and obtained through the courtesy of Dr. R.M. Nattrass.

Strain I. Isolated in 1951 from tomatoes growing in Peru and obtained through the courtesy of Miss C. Bazan de Segura.

Although many isolates from widely different sources have been tested, no additional new strains have been found. The vast majority of the isolates collected caused reactions in the differential hosts similar to the common strain A, but of the remainder, three were indistinguishable from B^1, two from B^2, one from C and one from D.

The method employed in the routine tests of seedling progenies was devised to provide approximately the optimum conditions for the growth of the parasite, viz. a temperature of 19° C. with relative humidity approaching 100 per cent. The temperature was controlled by using a glasshouse fitted with adequate heating and ventilation and a shading device to exclude /

exclude direct sunlight. To maintain the necessary humidity the seedlings to be tested were transplanted into boxes containing moist sterilised peat, and these in turn were placed in a shallow tank with a close-fitting lid. In that position the seedlings were sprayed, by means of an atomiser, with a spore suspension of the appropriate strain of the fungus. The lid was then closed. After approximately sixteen hours the boxes were removed from the tank and the plants exposed to the ordinary atmospheric conditions of the shaded glasshouse. There they remained for about five days, when lesions appeared on the susceptible segregates. The boxes were then replaced in the tank to promote abundant sporulation and so facilitate scoring. This method proved to be effective in killing off the susceptible segregates without causing serious harm to the resistant survivors. The latter may be retested with a different strain if so desired. At the completion of the tests the survivors were transplanted and grown to maturity in the ordinary way.

For certain purposes detached leaves were used instead of plants. The leaves were laid flat on moist peat in boxes, sprayed as before and covered with a suitable lid. They remained in this position for about seven days, when they were ready for scoring. This method is very convenient for the multiplication of fungal strains on leaves of their appropriate host plants. Cultural conditions advocated by Crosier (1933) were employed as a basis for the development of the above methods.

NATURE OF RESISTANCE.

The features of plants which are significant in disease resistance or susceptibility mechanisms constitute a complex comprising in the general case the effect of numerous morphological characteristics. Among these, for example, are thickness of cuticle, density of pubescence, osmotic concentration of sap, physiological sensitiveness of cells, etc. The protective agencies may differ in different varieties, resulting by their combined effect, in the appearance of many different degrees of resistance. In such circumstances a number of genetic factors must contribute towards the natural resistance of a variety and determine its ultimate reaction to attack.

The various characters which contribute towards resistance may be divided into two main groups: (1) those which determine the resistance of the plant to infection, and (2) those which determine the reaction of the plant after infection has occurred. The former group is represented in varieties of S. tuberosum and probably also in most potato species. In commercial varieties of S. tuberosum, all of which are attacked by the parasite, this group determines the degree of susceptibility and hence the amount of damage suffered. The second group is found in certain wild species of Solanum indigenous to Central and South America. In these, resistance is manifested in plants which respond to infection by developing a local necrosis which causes the invading organism to be

localised /

localised where it fails to develop and eventually dies. Plants of this type are known as hypersensitive or field immune.

The most promising species in this respect on the basis of experimental results appears to be S. demissum, a wild hexaploid form with many non commercial characteristics. This species has been used by many breeders during the last two decades. It comprises a number of varieties, some of which are hypersensitive and some susceptible to Phytophthora infestans. The hypersensitive varieties, when attacked, react quickly and necrotic spots appear at the points of entry of the fungus.

This hypersensitive reaction has been examined by Müller (1941) who found that resistance genes function only as accelerators of the defence reaction, of which both susceptible and resistant genotypes are capable. In other words, the genes confer control by affecting the sensitiveness of the cells to the presence of the fungus. Müller, Meyer and Klinkowski (1939) showed that it is possible to distinguish in this defence necrosis at least five successive stages, the last two being characterised by cell collapse. This kind of reaction or train of events, according to Müller and Boerger (1941), is not confined to members of the genus Solanum. The influence of temperature on this reaction was found by Müller and Griesinger (1942) to be considerable. At low temperatures the reaction of susceptible plants strongly resembled that of resistants but no decrease in the capacity for resistance

in /

in the resistant genotypes was induced. The effect of narcotics on the immunological behaviour of plants was studied by Müller and Behr (1949) and found to be similar to that resulting from low temperature treatment.

The term "resistance", being a general term, is apt to be misleading since it may apply to any of the factors providing natural protection from damage to a plant by a pathogen. Through lack of a better term, it is retained in the present work where it refers specifically to the protection afforded by hypersensitivity inherited from S. demissum.

CYTOGENETICAL BASIS OF INHERITANCE.

The cytogenetical basis of inheritance in potatoes has for long been the subject of controversy. Earlier work was interpreted on the assumption that the cultivated potato behaved as a diploid but investigations of New World potatoes, following the first Russian expedition to South America in 1925, established the well-known polyploid series into which potatoes are now grouped. This series, consisting of somatic chromosome numbers of 24, 36, 48, 60 and 72, suggests that the basic chromosome number in the potato family is 12. Several authors, e.g. Muntzing (1933), Ellison (1936a), Emme (1936) and Choudhuri (1943) suggested that the basic chromosome number, on the evidence of secondary associations at meiotic metaphase, might be 6. This suggestion however, through lack of further evidence, was not widely accepted and the basic chromosome number is now regarded as 12 by most workers.

That commercial varieties of S. tuberosum are auto-tetraploids was suggested by Lunden (1937) on the evidence of considerable data of the inheritance of pigmentation and other characters in this species. Cadman (1942) also explained results concerning the inheritance of reaction to virus X using a similar concept. The opposite view, that S. tuberosum is allopolyploid in constitution was put forward by Meurman and Rancken (1932) and Ellison (1935) when they found that somatic cells of certain varieties of S. tuberosum possessed not more than two satellite-carrying chromosomes. Juzepczuk

and Bukasov (1929) as a result of a survey of the geographical distribution of species, and Longley and Clark (1930) in cytological investigations of cultivated varieties also considered S. tuberosum to be of mixed origin. Investigations carried out by Thomas (1945) showed that in cultivated potatoes there is an average of less than two true quadrivalents per nucleus and consequently he concluded that the species is an allotetraploid hybrid between related species whose chromosomes are structurally similar.

In S. demissum (2n = 72) 36 bivalents were observed by Smith (1927) and Longley and Clark (1930). Cooper and Howard (1952) found that quadrivalents do not occur with a frequency of more than one per nucleus and regarded S. demissum as an allohexaploid.

In hybrids of S. demissum (2n = 72) and S. tuberosum (2n = 48), Mary Adams (in Salaman 1928), observed that 24 bivalents and 12 univalents were formed. Becker (1939) and Schnell (1948) suggested that more than 24 bivalents and less than 12 univalents may occur. This seems probable in the light of the results of Bains and Howard (1950) and Dodds (1950), who found that in haploid plants of S. demissum 2 to 7 bivalents per nucleus were formed. The evidence of Thomas (1945) that tetraploid hybrids of S. Rybinii (2n = 24) and S. demissum (2n = 72) and of (S. Rybinii x S. demissum) X S. tuberosum (2n = 48) had a meiotic behaviour very similar to S. tuberosum itself, indicates that the different sets of chromosomes are similar enough to pair. It seems probable that pairing in such /

hybrids usually takes place between corresponding chromosomes of different species, but that in certain circumstances pairing may occur between chromosomes of different sets of the same species. The weight of evidence favours the mixed origin of S. demissum and S. tuberosum with 12 as the basic chromosome number. Accordingly S. tuberosum (2n = 48) is regarded as fundamentally an allotetraploid and S. demissum (2n = 72) as an allohexaploid for the purposes of the present investigations.

EXPERIMENTAL RESULTS.

Differentiation of Genotypes by Specialised Fungal Strains.

In the course of the experiments the common strain and nine specialised strains of *P. infestans* were employed in testing the foliage of potato varieties and seedling progenies bred from *S. demissum* for resistance to the disease. The results showed that resistance, due to the hypersensitive condition of the protoplasm, is manifested in the presence of major genetic factors or genes derived from this wild species and that four such genes, viz. R_1, R_2, R_3 and R_4, have been distinguished in this material. Each gene when present in the plant induces a hypersensitive response to infection with the common strain and with a particular group of specialised strains of the parasite. These genes are inherited independently in simple Mendelian fashion. Examination of the reactions of the four genotypes suggests that the relationships between genes in the potato and fungal strains form a definite pattern as indicated in Table 1. The strains may be divided into four groups according to the number of genes inducing resistance to them. Thus four genes provide resistance to strain A, three to strains B^1, H and D, two to strains G, E, B^2, C and I, and one to strain F.

TABLE 1. /

TABLE 1.

GENES	STRAINS									
	A	B^1	H	D	G	E	B^2	C	I	F
R_1	−	+	−	−	+	+	+	−	−	+
R_2	−	−	+	−	+	−	−	+	−	−
R_3	−	−	−	−	−	+	−	−	+	+
R_4	−	−	−	+	−	−	+	+	+	+

− = Resistant + = Susceptible

Reactions of Resistant Plants Used as Parents.

The blight resistant varieties and seedlings employed as parents in the experiments to be discussed, together with their reactions, where known, to the ten strains of P. infestans, are listed in Table 2. The genetic constitution of each is shown in the last column.

TABLE 2.

REACTIONS OF RESISTANT VARIETIES AND SEEDLINGS USED AS PARENTS.

REFERENCE	REACTIONS TO STRAINS A B^1 B^2 C D E F G H I	GENOTYPES (Significant Terms only)
Aquila	R s s R R s s s R R	R_1
Falke	R s s R R s s	R_1
Jakobi /		

TABLE 2 (contd.)

REFERENCE	REACTIONS TO STRAINS A	B^1	B^2	C	D	E	F	G	H	I	GENOTYPES (Significant Terms only)
Jakobi	R	s	s	R	R	s	s				R_1
Kennebec	R	s	s	R	R	s	s	s	R	R	R_1
Robusta	R	s	s	R	R	s	s				R_1
W800(2)	R	s	s	R	R	s	s				R_1
W967c(38)	R	s	s	R	R	s	s				R_1
429a(1)	R	R	R	R	R	R	R				Ra(Ra)Rb(Rb)
(4)	R	R	R	R	R	R	R				Ra(Ra)Rb(Rb)
(6)	R	R	R	R	R	R	R				Ra(Ra)Rb(Rb)
(8)	R	R	R	R	R	R	R				Ra(Ra)Rb(Rb)
429b(5)	R	R	R	R							Ra(Ra)Rb(Rb)
556a(30)	R	R									Ra(Ra)Rb(Rb)
556b(2)	R	R									Rb
(4)	R	R									(Ra)Rb
568(18)	R	R									(Ra)Rb
571(18)	R	R									(Ra)Rb
(31)	R	R									Rb
594(10)	R	s									R_1
(86)	R	s									R_1
651(10)	R	s									R_1
653a(115)	R	s									R_1
(140)	R	s									R_1
653b(103)	R	s									R_1
653c(35)	R	s	s	R							R_1
653e(22)	R	s									R_1
(25)	R	s									R_1
655(34)	R	s	s	R							R_1
(39)	R	s									R_1
(43)	R	s	s	R							R_1
684a(13)	R	R									(Ra)Rb
(49)	R	s									Ra
686a(66)	R	R									(Ra)Rb
687b(10)	R	s									(Ra)
(29)	R	s									(Ra)
691a(39)	R	s									(Ra)
(80)	R	s									(Ra)
692a(29)	R	s									(Ra)
(52)	R	R									(Ra)Rb
692b(12)	R	R									(Ra)Rb
693a(43)	R	R									(Ra)Rb
(44)	R	R									Rb
(59)	R	R									Rb
(101)	R	R									Rb
735	R	R	R	R	R	R	R	R	R	R	$R_1R_2R_3R_4$
742b(2) /											

TABLE 2 (contd.)

REFERENCE	REACTIONS TO STRAINS A	B^1	B^2	C	D	E	F	G	H	I	GENOTYPES (Significant Terms only)
742b(2)	R	s									Ra
759b(5)	R	s									R_1
762(1)	R	s									R_1
764a(15)	R	s									R_1
764c(11)	R	s									R_1
833a(25)	R	s									R_1
834b(6)	R	s	s	R	R	s	s				R_1
834c(29)	R	s	s	R	R	s	s				R_1
835a(4)	R	s	s	R	R	s	s	s	R	R	R_1
850a(24)	R	s									R_1
855(14)	R	s									R_1
877a(34)	R	R	R	s	R	R	R				R_2
882(5)	R	R	R	R	R	R	R				R_1R_2
884(1)	R	R									$R_1R?$
885(1)	R	s									R_1
(2)	R	R	R	R	R	s	s				R_1R_3
(3)	R	R									$R_3R?R?$
(4)	R	R	R	R	R	R	s	R	R	R	$R_1R_3R_4$
886(1)	R	R	R	s	R	R	R	R	R	R	R_2R_4
(2)	R	s									R_1
914a(12)	R	s	s	R	R	s	s	s	R	R	R_1
(91)	R	s	s	R	R	s	s	s	R	R	R_1
914b(52)	R	s	s	R	R	s	s	s	R	R	R_1
997a(4)	R	s									R_1
(5)	R	s									R_1
(25)	R	s									R_1
(30)	R	s									R_1
(44)	R	R	R	R	R	s	s				R_3
(51)	R	R	R	R	R	s	s				R_3
(61)	R	s									R_1
997d(16)	R	R	R	R	R	s	s				R_3
998a(7)	R	R	R	R	R	s	s				R_3
(18)	R	R	R	R	R	s	s				R_3
(43)	R	R	R	R	R	s	s				R_3
998c(10)	R	R	R	R	R	s	s				R_3
1092a(4)	R	s	s	R	R	s	s				R_1
1104a(3)	R	R	R	R	R	R	s	R	R	s	R_3R_4
(6)	R	R									R_1R_3 or R_3R_4
(16)	R	R									R_3
(23)	R	R									R_3
1104b(19)	R	R									R_3
1104c(2) /											

TABLE 2 (contd.)

REFERENCE	REACTIONS TO STRAINS A	B^1	B^2	C	D	E	F	G	H	I	GENOTYPES (Significant Terms only)
1104c(2)	R	R	R	R	R	R	s	R	R	s	R_3R_4
1253a(12)	R	R	R	R	R	s	s	R	R	s	R_3
(15)	R	R	R	R	R	s	s				R_3
1256a(23)	R	R	R	R	R	s	s				R3
1257a(7)	R	R	R	R							R3
1258a(19)	R	R	R	R	R	s	s				R3
1270a(5)	R	R	R	R							R3
(11)	R	R	R	R							R3
(15)	R	R	R	R							R3
(16)	R	R	R	R							R3
1270b(9)	R	R	R	R	R	s	s				R3
1271b(9)	R	R	R	R							R3
(11)	R	R	R	R							R3
1276a(1)	R	R	R	R							R3
(4)	R	R	R	R							R3
(12)	R	R	R	R							R3
1276b(6)	R	R	R	R	R	s	s				R3
(10)	R	R	R	R	R	s	s				R3
1306a(2)	R	R	R	R	R	R	s	R	R	s	R_3R_4
(15)	R	R	R	R	R	R	s				$R_3R_3R_4$
1307a(23)	R	R	R	R	R	s	s				R_3R_3
1315b(10)	R	R	R	s	R	R	R				R_2
1318(3)	R	R	R	s	R	R	R				R_2
1332a(6)	R	R	R	R							R3
1439a(4)	R	R	R	R	R	s	s				R3
1488b(1)	R	R	R	R	R	R	s	R	R	s	R_3R_4
1506b	R	R	s	s	s	R	s	R	R	s	R_4
1506b(9)	R	R	s	R	R	R	s	R	R	R	R_1R_4
1508b(3)	R	R	R	s	R	R	R				R_2
1509a(3)	R	R	R	s	R	R	R				R_2
(4)	R	R	R	s	R	R	R				R_2
1512c(11)	R	R	R	R	R	R	R	s	R	R	R_1R_2
(14)	R	R	R	s	R	R	R				R_2
(16)	R	R	R	s	R	R	R	s	s	R	R_2
1512d(4)	R	R	R	R	R	R	R	s	R	R	$R_1R_1R_2$
(11)	R	R	R	R	R	R	R	s	R		R_1R_2
1514a(1)	R	R	R	R	R	R	R				R_1R_2
1517a(1)	R	R	R	s	R	R	R				R_2
1517b(2)	R	R	R	R	R	R	R				R_1R_2
1518d(2)	R	R	R	s	R	R	R				R_2R_4
1521c(6)	R	R	R	R	R	R	R				$R_2R_3R_4$
1563a(5)	R	R	R	R	R	s	s				R3
(6)	R	R	R	R	R	s	s				R3
(18)	R	R	R	R	R	s	s				R3
1563b(8)	R	R	R	R	R	R	s				R_3R_4
1564a(9) /											

TABLE 2 (contd.)

REFERENCE	REACTIONS TO STRAINS A	B^1	B^2	C	D	E	F	G	H	I	Genotypes (Significant Terms only)
1564a(9)	R	R	R	R	R	R	s				R_3R_4
(12)	R	R	R	R	R	R	s	R	R	s	R_3R_4
(15)	R	R	R	R	R	R	s	R	R	s	R_3R_4
1567a(7)	R	R	R	R	R	R	s				R_3R_4
1573(10)	R	R	R	R	R	s	s	R	R		R_3
1584b(7)	R	R	R	R	R	R	s	R	R	s	R_3R_4
1584c(10)	R	R	R	R	R	R	s	R	R	s	R_3R_4
(16)	R	R	R	R	R	R	s	R	R		R_3R_4
1591a(19)	R	R	R	R	R	R	s				R_3R_4
1647b(1)	R	R	R	R	R	R	R	s	R	R	R_1R_2
1682c(1)	R	R	R	R	R	R	R	R	R	R	R_2R_3
1786a	R	R	s	s	s	R	s	R	R	s	R_4

Inheritance of Resistance.

Multiple Hybrid Material: Gene R_1.

The progenies to be discussed in this group of material were derived from the fifth generation seedling W800(2) (Fig. 1). Since the first five generations were bred and raised by the late Dr. Wilson at St. Andrews, the writer has no information regarding their reactions to infection with blight. Seedling W800(2), however, proved to be hypersensitive to strains A, C and D, but susceptible to B^1, B^2, E and F. Although it possessed several undesirable characters it was highly self fertile. No critical cytological examination of W800(2) has been attempted but chromosome counts of it and of a number of its derivatives which were subsequently employed as /

as parents showed that in neither root tip nor pollen-mother-cell preparations was there any deviation from 48 somatic or 24 gametic chromosome complements.

When Dr. Wilson was engaged in interspecific hybridisation of potatoes little was known regarding the systematics of the tuber-bearing Solanums and few species had been described. On the authority of Dr. R.N. Salaman, privately communicated, the plants which Dr. Wilson described as S. tuberosum (Mexican sp.) and S.etuberosum were in reality S. demissum and S. edinense respectively. Thus the five species involved in the breeding of W800(2) were S. commersonii, S. maglia, S. edinense, S. demissum and S. tuberosum. The family tree of W800(2) was first published by Robb (1921) and it is here reproduced in Fig. 1 with the two corrections in classification.

W800(2) was found to possess a single gene conferring resistance to strains A, C and D. This gene is designated R_1. The segregation obtained by selfing W.800(2) (Table 3) shows a significant deviation from the expected 3 : 1 ratio in favour of recessives. Likewise an excess of susceptible plants resulted from the crossing of W.800(2) with cultivated varieties where a 1 : 1 ratio was expected. A seedling W.967c(38), bred from W.800(2) and Bishop, was used extensively as female parent in crosses with various susceptible varieties and seedlings. The results of the progeny tests (Table 4) again show a definite excess of recessives. These segregations indicate that W.800(2) and its backcross seedling W.967c(38) are similarly constituted in /

in respect of the blight-resistance character. It is worthy of note that the segregations obtained were similar although W.800(2) was employed as male parent and W.967c(38) as female parent in their respective hybridisations. Accordingly reciprocal crosses can be assumed to behave in similar fashion.

Table 5 contains a series of progenies representing the third backcrossed generation from W.800(2). In all cases a 1 : 1 ratio was expected. All but 6 progenies show an excess of recessives and the mean deviation in favour of recessives is smaller than was obtained in the progenies bred directly from W.800(2) and W.967c(38).

TABLE 3.

Ist-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN **A**.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (Significant Terms only)
937	W.800(2) B.S.	237	134	1.77 : 1	3 : 1	R_1
833-5	Craigs Defiance x W.800(2)	500	637	0.78 : 1	1 : 1)	
837	Epicure x W.800(2)	79	132	0.60 : 1	1 : 1)	
1076	Great Scot x do.	73	143	0.51 : 1	1 : 1)	r x R_1
1077	Imperia x do.	182	255	0.71 : 1	1 : 1)	
1079	Ninetyfold x do.	68	78	0.87 : 1	1 : 1)	
		902	1245	0.72 : 1	1 : 1	

B.S. = Bagged Self.

TABLE 4./

TABLE 4.

2ND-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (Significant Terms only)
652	W.967c(38) x Flourball	29	44	0.66 : 1	1 : 1)	
653	do. x Katahdin	207	269	0.77 : 1	1 : 1)	
655	do. x 70(13)	54	67	0.81 : 1	1 : 1)	
759	do. x The Alness	153	176	0.87 : 1	1 : 1)	
760	do. x Liddesdale Lad	50	60	0.83 : 1	1 : 1)	R_1 x r
761	do. x Pepo	60	92	0.65 : 1	1 : 1)	
763	do. x Shamrock	57	54	1.06 : 1	1 : 1)	
764	do. x 121(2)	199	225	0.88 : 1	1 : 1)	
855	do. x M.233(13)	45	44	1.02 : 1	1 : 1)	
1095	do. x T(a)	71	88	0.81 : 1	1 : 1)	
		925	1119	0.83 : 1	1 : 1	

Segregations resulting from the selfing of one 1st- and five 2nd-generation seedlings derived from W.800(2) are set out in Table 6. The proportions of resistants to susceptibles are somewhat variable, ranging from 2.00 : 1 to 3.76 : 1, but the mean deviation shows a comparatively small though definite excess of recessives compared with the expected 3 : 1.

TABLE 5. /

TABLE 5.

3RD-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
839	594(86) x Liddesdale Lad	55	59	0.93 : 1	1 : 1	R_1 x r
1081	651(10) x M.233(13)	51	65	0.78 : 1	1 : 1	do.
1082	do. x T(a)	132	144	0.92 : 1	1 : 1	do.
844	653a(115) x Gladstone	53	36	1.47 : 1	1 : 1	do.
845	do. x Liddesdale Lad	65	76	0.86 : 1	1 : 1	do.
847	do. x Pepo	60	42	1.43 : 1	1 : 1	do.
850	653a(140) x The Alness	39	45	0.87 : 1	1 : 1	do.
919	653b(103) x do.	76	76	1.00 : 1	1 : 1	do.
923	do. x Edgecote Purple	36	52	0.69 : 1	1 : 1	do.
924	do. x Kepplestone Kidney	112	105	1.07 : 1	1 : 1	do.
925	do. x Pepo	92	86	1.07 : 1	1 : 1	do.
1092	653e(22) x T(a)	78	85	0.92 : 1	1 : 1	do.
927-8	653e(25) x The Alness	63	69	0.91 : 1	1 : 1	do.
930	do. x Pepo	40	51	0.78 : 1	1 : 1	do.
931	655(34) x The Alness	68	90	0.76 : 1	1 : 1	do.
934	655(39) x Suttons Early Regent	168	197	0.85 : 1	1 : 1	do.
1093	759b(5) x Cardinal	58	59	0.98 : 1	1 : 1	do.
		1246	1337	0.93 : 1	1 : 1	

TABLE 6. /

TABLE 6.

SELFED DERIVATIVES OF MULTIPLE HYBRID W.800(2)

TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEORETICAL	GENOTYPES (Significant Terms only)
856	594(10) N.S.	128	34	3.76 :1	3 : 1	R_1
1096	762(1) N.S.	143	48	2.98 :1	3 : 1	R_1
936	764a(15) N.S.	144	45	3.20 :1	3 : 1	R_1
1329	834b(6) N.S.	93	37	2.51 :1	3 : 1	R_1
1098	850a(24) N.S.	116	58	2.00 :1	3 : 1	R_1
1099	855(14) N.S.	136	50	2.72 :1	3 : 1	R_1
		760	272	2.79 :1	3 : 1	

N.S. = Natural Self.

A number of progenies, obtained by crossing W.800(2) and some of its derivatives with recessive varieties, were tested with the C strain in order to compare the segregations with these previously observed in the A strain experiments. The segregations in the C strain tests are shown in Table 7. They approximate to a 1 : 1 ratio, deviating steadily towards an excess of recessives, and are comparable with the ratios previously obtained with the A strain of the fungus.

TABLE 7. /

TABLE 7.

DERIVATIVES OF W.800(2) TESTED WITH STRAIN C.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	SUGGESTED GENOTYPES (DOMINANT GENES ONLY)
835b	Craigs Defiance x W.800(2)	75	94	0.80 : 1	1 : 1	
1411a	Majestic x 834b(6)	31	29	1.07 : 1	1 : 1	r x R_1
1412e	do. x 834c(29)	90	150	0.60 : 1	1 : 1	
1415b	653c(35) x Katahdin	102	103	0.99 : 1	1 : 1	
1416b	do. x Dr McIntosh	57	71	0.80 : 1	1 : 1	
1417e	do. x 910a (123)	42	63	0.67 : 1	1 : 1	
1418e	655(43) x Katahdin	24	32	0.75 : 1	1 : 1	R_1 x r
1419d	do. x Dr McIntosh	39	53	0.74 : 1	1 : 1	
1423a	834b(6) x Katahdin	158	129	1.22 : 1	1 : 1	
1425b	835a(4) x do.	81	83	0.98 : 1	1 : 1	
		699	807	0.87 : 1	1 : 1	

That resistance is due to the presence of one major gene is confirmed by the fact that no seedling which survived the A strain test was found to be susceptible to C, and similarly no survivor of the C strain test proved to be susceptible to strain A.

Further segregations involving the gene R_1 are shown in Table 8, where strain C was employed for test purposes. Seedling 834c(29) and Aquila are the R_1 types, and when these are /

were crossed with recessives the progenies again showed a slight majority of susceptible segregates. The seventy-seven survivors of the C strain test in progeny 1978a (Aquila Selfed) were also inoculated with strain D, but as anticipated they all proved resistant.

TABLE 8.

DERIVATIVES OF MULTIPLE HYBRID W.800(2) AND OF AQUILA TESTED WITH STRAIN C.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (Significant Terms only)
1481d	791a(116) x 834c(29)	52	58	0.90 : 1	1 : 1	r x R_1
1906ab	King Edward VII x Aquila	32	43	0.74 : 1	1 : 1	r x R_1
1978ab	Aquila Selfed	195	51	3.82 : 1	3 : 1	R_1

Further reference to the deviations from standard Mendelian ratios observed in progenies bred from W.800(2) will be made in the Discussion.

S. demissum-S. tuberosum Hybrids: Gene R_2.

The second type of resister, exemplified by seedling 877a(34), was found to possess a single gene designated R_2 which confers resistance to strains A, B^1, D, E, B^2, and F. In Table 9 are shown the segregations obtained in progenies derived from 877a(34) and 1318(3) (Fig. 2) where the three strains, /

strains, A, B^2 and C, were separately employed. The female parent in the crosses is a recessive type in each case.

Seedling 877a(34) is resistant to strains A and B^2 but susceptible to C. The progeny from which it was selected, viz. 877, was tested with strain A (see Table 18), and segregated 129 resistants : 130 susceptibles — a close approximation to a 1 : 1 ratio. A further quantity of seed from the same cross (Ref. No. 877d) was sown to provide plants for C strain test.

TABLE 9.

DERIVATIVES OF 877a(34) TESTED WITH STRAINS A, B^2 AND C.

REF. NO.	PARENTAGE	STRAIN	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1330a	877a(34) N.S.	A	111	26	4.27 : 1	3 : 1	R_2
1315abc	Epicure x 877a(34)	A	301	336	0.90 : 1	1 : 1	r x R_2
1318	Craigs Defiance x 877a(34)	A	74	89	0.83 : 1	1 : 1	
1321abc	Ninetyfold x 877a(34)	A	142	199	0.71 : 1	1 : 1	
			517	624	0.83 : 1		
1444	British Queen x 877a(34)	B^2	29	30	0.97 : 1	1 : 1	
1648ab	Southesk x 1318(3)	B^2	148	177	0.84 : 1	1 : 1	r x R_2
1650) 1651a)	831(113) x 1318(3)	B^2	156	183	0.85 : 1	1 : 1	
			333	390	0.85 : 1		
1619c	877a(34) N.S.	C	0	99	..	0 : 00	R_2
1727a	1318(3) N.S.	C	1	173	..	0 : 00	

N.S. = Natural Self.

Eighty-seven seedlings were inoculated and all proved to be susceptible. It is apparent from these results that 877a(34) possesses the gene R_2 in the simplex condition, and that it should, on crossing with recessive types, give progenies which segregate resistants and susceptibles in equal proportions, irrespective of whether the A or the B^2 strain of the fungus is used. This is confirmed in Table 9. Seedling 1318(3), which was bred from 877a(34), gave similar results in the B^2 strain tests but was not included in the experiments with strain A.

Further confirmation of the presence of the gene R_2 was obtained from selfed progenies of 877a(34), in which a ratio of 3 resistants : 1 susceptible resulted from inoculation with strain A, but with strain C all the individuals proved to be susceptible. The selfed progeny of 1318(3) was also expected to succumb to strain C, and 173 of the 174 plants did so. It is presumed that the single survivor was a rogue plant.

The intercrossing of R_2 plants with R_1 plants might be expected to produce three different resistant genotypes in the offspring. Tests of such progenies with strains B^2 and C independently (Table 10) show that in both cases the segregations approximate equality. When, however, the survivors of the B^2 strain test are inoculated with strain C, approximately half of their number succumb (Table 11). Similarly when the survivors of the C strain test are inoculated with strain B^2 approximately half of their number are killed (Table 12). Apparently /

Apparently the plants segregate in the proportion of

1 R_1R_2 : 1 R_1 : 1 R_2 : 1 r.

TABLE 10.

DERIVATIVES OF 877a(34) AND W.800(2) TESTED WITH STRAINS B^2 AND C.

REF. NO.	PARENTAGE	STRAIN	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1647ab	655(43) x 1318(3)	B^2	38	53	0.72 : 1	1 : 1	$R_1 \times R_2$
1658a) 1659a)	835a(4) x 1318(3)	B^2	166	146	1.14 : 1	1 : 1	$R_1 \times R_2$
1678ab	1092a(4) x 1318(3)	B^2	105	111	0.95 : 1	1 : 1	$R_1 \times R_2$
1697a	1315b(10) x 834c(29)	B^2	93	90	1.03 : 1	1 : 1	$R_2 \times R_1$
			402	400	1.01 : 1		
1659c	835a(4) x 1318(3)	C	104	95	1.09 : 1	1 : 1	$R_1 \times R_2$
1678c	1092a(4) x 1318(3)	C	52	50	1.04 : 1	1 : 1	$R_1 \times R_2$
1697b	1315b(10) x 834c(29)	C	149	161	0.93 : 1	1 : 1	$R_2 \times R_1$
			305	306	1.00 : 1		

If strain B^2 is applied first, the R_1 and the recessive individuals are killed. Subsequent inoculation of the survivors with strain C destroys the R_2 plants, leaving only the R_1 R_2 types alive. When the order of inoculation is reversed, the C strain kills the R_2 and the recessive plants, while the B^2 strain destroys the R_1 types. Again only the R_1 R_2 segregates, representing approximately 25 per cent. of the original progeny, remain /

remain alive.

TABLE 11.

DOUBLE TEST (STRAIN B^2 FOLLOWED BY STRAIN C).

REF. NO.	PARENTAGE		KILLED BY B	KILLED BY C	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1647ab	655(43) x 1318(3)	O	53	19	19	
		E	45.5	22.75	22.75	
1658a	835a(4) x 1318(3)	O	81	33	53	$R_1 \times R_2$
		E	83.5	41.75	41.75	
1678a	1092a(4) x 1318(3)	O	66	33	28	
		E	63.5	31.75	31.75	
1697a	1315b(10) x 834c(29)	O	90	45	48	$R_2 \times R_1$
		E	91.5	45.75	45.75	

O = Observed. E = Expected.

TABLE 12.

DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B^2).

REF. NO.	PARENTAGE		KILLED BY C	KILLED BY B	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1659c	835a(4) x 1318(3)	O	95	52	52	$R_1 \times R_2$
		E	99.5	49.75	49.75	
1678c	1092a(4) x 1318(3)	O	50	27	25	$R_1 \times R_2$
		E	51	25.5	25.5	
1697b	1315b(10) x 834c(29)	O	161	70	79	$R_2 \times R_1$
		E	155	77.5	77.5	

O = observed. E = expected.

Additional /

Additional results, obtained from progenies resulting from the selfing of an R_2 type and from the crossing of R_1 and R_2 types, are shown in Table 13. Since the R_1 gene is ineffective against strain E, the simple 3 : 1 segregations for selfs and 1 : 1 for crosses were obtained. These results are similar to those previously obtained with strain B^2. The ninety-four plants of progeny 1979ab which survived the E strain test were later inoculated with strain F, but all, as expected, proved to be resistant.

TABLE 13.

DERIVATIVES OF 877a(34) TESTED WITH STRAIN E.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1979ab) 1818a)	877a(34) Selfed	148	68	2.18 : 1	3 : 1	R_2
1660ab	835a(4) x 1318(3)	157	146	1.08 : 1	1 : 1	$R_1 \times R_2$
1697c	1315b(10) x 834c(29)	99	88	1.13 : 1	1 : 1	$R_2 \times R_1$
		256	234	1.09 : 1		

Seedling 877a(34) was bred from S. demissum x S. tuberosum as shown in Fig. 2. When the earlier generations of this material were tested only strain A was available but later strain B^1 was isolated and some of the parent plants were also tested with it. In these circumstances, although it was possible to ascertain the number of R genes present in resistant parent plants, it was impossible to identify these genes with accuracy. Accordingly /

Accordingly the genes referred to in Tables 14 - 18 will be labelled either Ra or Rb to signify resistance to strain A or strain B[1] respectively.

S. demissum, used as female parent, was successfully crossed with pollen of cultivated varieties of S. tuberosum. All attempts to effect the reciprocal cross failed. The F_1 plants were only partially self-fertile, and several small F_2 families which were obtained did not provide satisfactory data for genetical analysis. A few resistant F_2 segregates were, however, used for further breeding. The F_1 progenies obtained by crossing S. demissum with S. tuberosum were resistant to both strains of blight. Various backcrossed progenies (F_1 x S. tuberosum var. Alness) were tested with the A strain of blight and the results are shown in Table 14.

TABLE 14.

F_1 x Susceptible

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
429a(1) x S. tuberosum	861,938	61	22			
429a(4) x do.	862,939	43	15			
429a(6) x do.	940	45	14			Ra(Ra)
429a(8) x do.	864	54	16			Rb(Rb)
do. x do.	736	67	26			x
do. x do.	941	98	16			r
429b(5) x do.	738	77	18			
	Total	445	127	3.5 : 1	> 3 : 1	

The observed ratios proved to be slightly inconsistent, but the totals /

totals gave a ratio of approximately 3.5 resistants to 1 susceptible. The results obtained by Reddick (1934) using the strain of blight prevalent in the U.S.A., presumably equivalent to the A strain used here, were very similar.

The theoretical backcross ratio, however, can hardly be calculated. The F_1 hybrids had 60 chromosomes and their behaviour at meiosis was irregular. Salaman (1928) found in the F_1 from similar parentage 24 bivalents and 12 univalents, and frequently one or more univalents were displaced at metaphase and appeared to lie outside the spindle. Becker (1939) also observed considerable irregularities at meiosis, including frequent non-orientated and lagging chromosomes.

In the experiments of Puskarev (1937) the F_1 hybrids between S. demissum and S. tuberosum had 60 chromosomes, but in backcrossed plants the numbers ranged from 50 to 60. The pollen grains of the male parent carried 24 chromosomes, therefore the numbers in the female gametes of the F_1 must have ranged from 26 to 36, showing a loss of univalents up to 10.

It has been observed that plants closely resembling the cultivated parent have fewer chromosomes than those exhibiting many characters of the wild form. Salaman (1928) found that derivatives of S. demissum x S. tuberosum which had 6-12 univalents approached the wild parent in general type, while those with less than 6 univalents resembled S. tuberosum more /

more closely. These observations indicate that genes for wild characters are carried by the univalent chromosomes. That genes for all the characters distinguishing the two species are carried by the unpaired demissum chromosomes must be false since blight-resistant plants with only 48 chromosomes have been obtained. However, it is apparent that many typical demissum characters are controlled by genes in the univalents, and if chance determines the frequency of the univalents in the offspring, the resulting segregations will vary accordingly.

The work of McClintock and Hill (1931) and others has shown that when a bivalent and a univalent are formed instead of a trivalent, the univalent may or may not be included in the first and second divisions. If it is lost in the cytoplasm through not being included on the spindle, the number of X gametes will be increased at the expense of the X+1 gametes.

In backcrossing the F_1 to S. tuberosum, it appears that as many as 10 of the 12 univalents are liable to be lost. Consequently genes for resistance to blight are likely to disappear and the number of susceptible segregates in the progeny will be increased at the expense of the resistants. The frequency with which the univalents carrying genes for blight resistance are included in the nucleus will affect the proportions of resistant phenotypes obtained, and this will therefore be greater than the theoretical output of the paired chromosomes. In the Tables the genes probably borne by univalent chromosomes are shown in brackets.

Since four different genes have, in later experiments, been /

been identified in S. demissum, they would all be expected to be present in the heterozygous condition in F_1 seedlings of S. demissum x S. tuberosum. When such F_1 seedlings (2n = 60) are backcrossed to S. tuberosum (2n = 48), one or more may be lost if located in univalent chromosomes, and the segregation ratios would vary accordingly. The ratios obtained in progenies bred from F_1 x susceptible (Table 14) show that the average distribution was 3.5 resistants : 1 susceptible, a ratio which suggests that two of the four genes were borne by unpaired chromosomes and that these were seldom transmitted to the progeny.

The segregations obtained in second backcrossed progenies are shown in Table 15. The three resistant seedlings used as parents gave distinctly different ratios in their progenies. Three different genotypes are therefore involved, since the male parents are all recessive. The ratios, however, show some deviation from normal Mendelian segregation and these deviations may again be explained by the presence of univalent chromosomes. In a cytological examination of one of the parents, 556a(30), 53 chromosomes were counted in a root-tip preparation. The presence of a blight-resistance gene in one of these extra chromosomes could account for the observed deviations.

TABLE 15. /

TABLE 15.

RESISTANT (F_1 x SUSCEPTIBLE) x SUSCEPTIBLE.

PARENTAGE	Ref. No.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
556a(30) x S. tuberosum	767	58	10	5.8 : 1	< 7 : 1	Ra(Ra)Rb x r
556b(2) x S. tuberosum	683) 740)	85	91	0.93 : 1	< 1 : 1	Rb (1) x r
556b(4) x S. tuberosum	684) 741) 742)	210	82	2.6 : 1	< 3 : 1	(Ra)Rb (2) x r

(1) Several of the A resistant seedlings were tested with the B^1 strain. All were resistant.

(2) Several of the A resistant seedlings were tested with the B^1 strain. Both resistants and susceptibles were present.

The results obtained in third backcrossed progenies are shown in Table 16. All these families can be traced back to a common resistant ancestor, 556b(4), included in Table 15, which was credited with the Ra gene in an unpaired chromosome and the Rb gene in a paired chromosome. The results show that two of the three possible resistant genotypes obtainable from it are represented in Table 16 and that all have inherited the univalent bearing the Ra gene. Tests made with the B^1 strain of blight served to confirm the presence or absence of the Rb gene.

Owing /

Owing to the low fertility of the F_1 hybrids, few F_2 seedlings were obtained. In a test involving 14 F_2 plants, 12 proved to be resistant and 2 susceptible. A ratio greater than 15 : 1 was expected. Three resistant F_2 seedlings were, however, backcrossed to S. tuberosum and the segregations in the resulting progenies are set out in Table 17. Two of the three plants were found to contain both an Ra and an Rb gene, and the segregations indicate that one of these genes was present in an unpaired chromosome. By further backcrossing, as shown in Table 18, it was found that the Ra gene was located in a univalent and that the Rb gene was contained in a paired chromosome. In a cytological examination of the resistant parent 571(18), 60 chromosomes were counted in the root tips.

TABLE 16.

RESISTANT (F_1 x SUSCEPTIBLE) x SUSCEPTIBLE x SUSCEPTIBLE.

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)	
684a(13) x S. tuberosum	770) 867) 868) 869)	251	108	2.3 : 1	$\lessgtr$ 3 : 1	(Ra)Rb x r	(1)
684a(49) x S. tuberosum	771) 772)	47	69	0.68 : 1	$\lessgtr$ 1 : 1	(Ra) x r	(2)

742b(2) /

TABLE 16 (contd.)

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)	
742b(2) x S. tuberosum	958) 959) 960)	190	289	0.65 : 1	1 : 1	(Ra) x r	(3)

(1) Several of the A resistant seedlings were tested with the B^1 strain. Both resistants and susceptibles were present.

(2) Several of the A resistant seedlings were tested with the B^1 strain. All were susceptible.

(3) 742b(2) was susceptible to the B^1 strain.

TABLE 17.

RESISTANT F_2 x SUSCEPTIBLE.

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)	
568(18) x S. tuberosum	686) 687)	242	142	1.7 : 1	3 : 1	(Ra)Rb x r	(1)
571(18) x S. tuberosum	691) 692) 693) 768)	266	136	1.9 : 1	3 : 1	(Ra)Rb x r	(1)
571(31) x S. tuberosum	694	81	79	1 : 1	1 : 1	Rb x r	

(1) /

(1) Several of the A resistant seedlings were tested with the B^1 strain. Both resistants and susceptibles were present.

Various progenies, which form a second backcrossed generation from the F_2, were raised and tested and the segregations are shown in Table 18. All the resistant parents were selected from progenies discussed in Table 17, in which the possible number of genotypes is limited to three. The effective genes involved in Table 17 are Ra and Rb, therefore the resistant parents in Table 18 may possess either or both. These three alternatives are sufficient to explain the segregations obtained, and the presence or absence of the Rb gene was confirmed by a number of tests with the B^1 strain of blight.

Cytological examination of three of the parent seedlings revealed the presence of extra chromosomes. 50 chromosomes were counted in root-tip preparations of 691a(39) and 692b(12), and 51 in 691a(80).

TABLE 18.

RESISTANT (F_2 x SUSCEPTIBLE) x SUSCEPTIBLE.

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)	
686a(66) x S. tuberosum	943	34	25	1.4 : 1	$< 3 : 1$	(Ra)Rb x r	(1)

687b(10) /

TABLE 18 (contd.)

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)	
687b(10) x S. tuberosum	948) 949)	34	62	0.55 : 1	< 1 : 1	(Ra) x r	
687b(29) x S. tuberosum	950) 951) 1100)	140	196	0.71 : 1	< 1 : 1	(Ra) x r	(2)
691a(39) x S. tuberosum	773	63	81	0.77 : 1	< 1 : 1	(Ra) x r	(3)
691a(80) x S. tuberosum	774) 775)	122	117	1.0 : 1	< 1 : 1	(Ra) x r	(3)
692a(29) x S. tuberosum	776	60	120	0.5 : 1	< 1 : 1	(Ra) x r	(3)
692a(52) x S. tuberosum	870) 872) 873) 874)	271	132	2.0 : 1	< 3 : 1	(Ra)Rb x r	(4)
692b(12) x S. tuberosum	777) 778)	147	71	2.0 : 1	< 3 : 1	(Ra)Rb x r	(4)

693a(43) /

TABLE 18 (contd.)

PARENTAGE	REF. NO.	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
693a(43) x S. tuberosum	779	86	30	2.86 : 1	3 : 1	(Ra)Rb x r
693a(44) x S. tuberosum	780) 782) 783) 784) 785)	179	193	0.93 : 1	1 : 1	Rb x r
693a(59) x S. tuberosum	786) 787)	89	80	1:1 : 1	1 : 1	Rb x r
693a(101) x S. tuberosum	877	129	130	1 : 1	1 : 1	Rb x r (5)

(1) 686a(66) was resistant to the B^1 strain.
(2) 687b(29) was susceptible to the B^1 strain.
(3) Several of the A resistant seedlings were tested with the B^1 strain. All were susceptible.
(4) Several of the A resistant seedlings were tested with the B^1 strain. Both resistants and susceptibles were present.
(5) Several of the A resistant seedlings were tested with the B^1 strain. All were resistant.

The loss of chromosomes in material bred from S. demissum x S. tuberosum and the consequent effect on segregation ratios has recently been observed by Cooper and Howard (1952). They found that the majority of seedlings in second, third and fourth backcross generations which they examined had from 49 to 54 chromosomes.

Triple Hybrids : Genes R_3 and R_4.

The third type of resister, exemplified by seedling 1253a(12), was found to possess a single gene, designated R_3, which confers resistance to strains A, B^1, B^2, C, D, G and H. This seedling is of triple hybrid origin, being derived from S. Rybinii (2n = 24), S. demissum (2n = 72) and S. tuberosum (2n = 48), and was selected from family 1253 shown in the pedigree (Fig. 3),

The scheme of breeding involving these three species was adopted in order to obtain at the outset blight-resistant plants with a balance complement of 48 somatic chromosomes. S. demissum pollen (n = 36) was applied to a large number of S. Rybinii flowers (n = 12) and eventually a berry containing one seed was obtained. This seed germinated to produce a self-fertile plant in which 48 somatic and 24 gametic chromosomes were observed. This plant (Ref. No. 735) was thereupon crossed with S. tuberosum varieties. The cross was not prolific but 8 berries were obtained, yielding a total of 12 seeds, 7 of which germinated. These triple hybrids were self-fertile and were readily backcrossed to S. tuberosum. Seedlings derived from the first backcrossed and subsequent generations proved to be highly fertile and prolific. In crossing with S. tuberosum they could be used either as male or female parent, and their utilisation has helped to overcome the sterility handicap in potato breeding. In an examination of this material, Thomas (1945) found that chromosome /

chromosome differentiation between these species was not sufficient to affect pairing to any extent and that the F_1 hybrid and the triple hybrids all had 48 somatic chromosomes. In crossing S. Rybinii (n = 12) with S. demissum (n = 36) it may be presumed that the 12 Rybinii chromosomes paired with 12 demissum chromosomes and that the remaining 24 demissum chromosomes paired amongst themselves. Thus 12 autosyndetic and 12 allosyndetic bivalents would be formed in a manner similar to that observed by Ellison (1936b) in other Solanum hybrids.

When the earlier generations were bred and tested, only two strains of blight, viz. A and B^1 were available. The results obtained in the F_1, triple hybrid and first back-cross generations are shown in Table 19. Reference to the genes concerned will be made later.

TABLE 19. /

TABLE 19.

REF. NO.	PARENTAGE	A STRAIN NO. OF SEEDLINGS R	A STRAIN NO. OF SEEDLINGS r	THEOR-ETICAL RATIO	B^1 STRAIN NO. OF SEEDINGS R	B^1 STRAIN NO. OF SEEDINGS r	THEOR-ETICAL RATIO	GENO-TYPES (SIG-NIFI-CANT TERMS ONLY)
735	S.Rybinii x S. demissum	1	0	∞: 0	1	0	∞: 0	r x R_1 $R_1R_2R_2$ $R_3R_3R_4R_4$
897	735 selfed	71	0	∞: 0	63	1	15: 1	$R_1R_2R_3R_4$
994	735 x S.Rybinii	16	0	∞: 0	14	2	3: 1	$R_1R_2R_3$ R_4 x r
884-6	735 x S.tuber-osum	7	0	∞: 0	5	2	3: 1	$R_1R_2R_3$ R_4 x r
995	884(1) x S.tuber-osum	21	6	3: 1	12	15	1: 1	R_1R?xr
996	885(1) x do.	94	99	1: 1	0	73	0: ∞	R_1 x r
997	885(2) x do.	216	75	3: 1	125	124	1: 1	R_1R_3xr
998	885(3) x do.	114	19	7: 1	121	44	3: 1	R_3R?R? x r
1112	885(3) selfed	75	0	63: 1	54	4	15: 1	R_3R?R?
1104	885(4) x S.tuber-osum	103	25	7: 1	78	33	3: 1	$R_1R_3R_4$ x r
1015	885(4) selfed	288	7	63: 1	31	0	15: 1	$R_1R_3R_4$
999	886(2) x S.tuber-osum	39	36	1: 1	0	52	0: ∞	R_1 x r
1016	886(2) selfed	42	16	3: 1	0	18	0: ∞	R_1

In the subsequent experimental work directly connected with this material, three of the triple hybrids, viz. 885(2), 885(3) and 885(4), were the main sources of resistance genes. It is proposed, therefore, to group the progenies on the basis of their relationships with these triple hybrids.

Triple Hybrid 885(2).

Seedling 1253a(12) (gene R_3) was selected in the second generation from 885(2). The progenies to be discussed in this generation /

generation are contained in Tables 20, 21, 22, 23, 24 and 25.

TABLE 20.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2)

TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEOR-ETICAL	GENOTYPES (SIGNIFI-CANT TERMS ONLY)
1286	997a(5)* N.S.	87	31	2.81:1	3:1	R_1
1287	997a(25)* N.S.	84	23	3.65:1	3:1	R_1
1288	997a(30)* N.S.	105	75	1.40:1	3:1	R_1
1289	997a(44)ø N.S.	95	48	1.98:1	3:1	R_3
1290	997a(51)ø N.S.	168	73	2.30:1	3:1	R_3
1331	997d(16)ø N.S.	200	88	2.27:1	3:1	R_3
1277	997a(4)* x 997a(5)*	62	30	2.07:1	3:1	R_1 x R_1
1278	997a(5)* x 997a(25)*	71	52	1.37:1	3:1	R_1 x R_1
1279	997a(5)* x 997a(61)*	78	48	1.63:1	3:1	R_1 x R_1
1280	997a(25)* x 997a(61)*	142	66	2.15:1	3:1	R_1 x R_1
1281	997a(30)* x 997a(61)*	67	38	1.76:1	3:1	R_1 x R_1
		1159	572	2.03:1	3:1	
1253	Craigs Defiance x 997a(44)ø	148	171	0.87:1	1:1	
1263	Golden Wonder x 997a(44)ø	90	108	0.83:1	1:1	
1267	Kerr's Pink x do.	80	85	0.94:1	1:1	r x R_3
1268	Majestic x do.	18	28	0.64:1	1:1	
		336	392	0.86:1	1:1	
1254	Craigs Defiance x 997a(51)ø	282	289	0.98:1	1:1	
1257	Di Vernon x do.	113	125	0.90:1	1:1	
1258	Epicure x do.	251	266	0.94:1	1:1	
1264	Golden Wonder x do.	65	104	0.63:1	1:1	r x R_3
1266	Katahdin x do.	59	65	0.91:1	1:1	
1269	Majestic x do.	64	64	1.00:1	1:1	
1270	Manxman x do.	201	258	0.78:1	1:1	
1271	Ninetyfold x do.	158	176	0.90:1	1:1	
1275	Southesk x do.	206	222	0.93:1	1:1	
		1399	1569	0.89:1	1:1	

* Resistant to A strain. Susceptible to B^1 strain.
ø Resistant to both A and B^1 strains.
N.S. Natural Self.

TABLE 21.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2) TESTED WITH STRAIN B^1.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1289	997a(44) N.S.	142	53	2.68:1	3:1	R_3
1435	Gladstone x 997a(44)	67	109	0.61:1	1:1	r x R_3
1620	997a(51) N.S.	265	96	2.76:1	3:1	R_3
1258	Epicure x 997a(51)	89	87	1.02:1	1:1)	r x R_3
1491	791a(116) x 997a(51)	98	125	0.78:1	1:1)	
		187	212	0.88:1	1:1	

N.S. = Natural Self.

TABLE 22.

COMPARISON OF SEGREGATIONS IN STRAIN A AND STRAIN B^1 TESTS.

PARENTAGE	A STRAIN SEEDLINGS TESTED	A STRAIN RATIO OBSERVED	A STRAIN RATIO THEORETICAL	B^1 STRAIN SEEDLINGS TESTED	B^1 STRAIN RATIO OBSERVED	B^1 STRAIN RATIO THEORETICAL
997a(44) Selfed	143	1.98:1	3:1	195	2.68:1	3:1
Susceptible x 997a(44)	728	0.86:1	1:1	176	0.61:1	1:1
997a(51) Selfed	241	2.30:1	3:1	361	2.76:1	3:1
Susceptible x 997a(51)	2968	0.89:1	1:1	399	0.88:1	1:1

TABLE 23. /

TABLE 23.

3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2)

TESTED WITH STRAIN B^2.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1679-80	1253a(12) x 834c(29)*	153	141	1.09:1	1:1	R_3 x R_1
1595	1253a(15) x Katahdin	33	24	1.37:1	1:1)	
1596	do. x Dr McIntosh	74	59	1.25:1	1:1)	R_3 x r
1684	do. x 834b(6)*	48	54	0.89:1	1:1	R_3 x R_1
		155	137	1.13:1	1:1	
1585	Southesk x 1257a(7)	104	97	1.07:1	1:1	r x R_3
1524	1258a(19) x 910a(123)	74	80	0.93:1	1:1)	
1605	do. x Pepo	69	85	0.81:1	1:1)	R_3 x r
		143	165	0.87:1	1:1	
G908	1270a(5) x Shamrock	41	57	0.72:1	1:1)	
G907	1270a(11) x do.	49	41	1.19:1	1:1)	
G909	do. (15) x do.	41	57	0.72:1	1:1)	R_3 x r
G910	do. (16) x do.	62	55	1.13:1	1:1)	
		193	210	0.92:1	1:1	
1688	1270b(9) x 910a(123)	104	108	0.96:1	1:1	R_3 x r
1687	do. x 834c(29)*	276	281	0.98:1	1:1	R_3 x R_1
		380	389	0.97:1	1:1	
1692	1271b(9) x 834c(29)*	51	78	0.65:1	1:1	R_3 x R_1
1681	1253a(12) x 1306a(2)ø	292	114	2.56:1	3:1)	
1598	do.(15) x do.	249	70	3.56:1	3:1)	
1689	1270b(9) x do.	245	88	2.78:1	3:1)	R_3 x R_3R_4
1693	1271b(9) x do.	87	31	2.81:1	3:1)	
1685	1253a(15) x 1332a(6)ø	275	119	2.31:1	3:1	R_3 x R_3
		1148	422	2.72:1	3:1	

* /

$\varkappa$ = Resistant to A strain but susceptible to B^1 strain (Table 3).
ϕ = Resistant to both A and B^1 strains (see Table 38).

Table 20 shows the segregations obtained by selfing, intercrossing, and backcrossing resistant seedlings selected in the 1st backcross generation of the triple hybrid 885(2) using strain A. Selfing and intercrossing resulted in segregations which, with one exception, showed an excess of recessives over the expected 3:1 ratio. The segregations varied rather widely, but the mean ratio was 2.03 resistants to 1 susceptible. "A" resisters and "B^1" resisters gave comparable results. Two of the "B^1" resistant seedlings, 997a(44) and 997a(51), were used as pollen parents in backcrossing to S. tuberosum varieties. A 1:1 ratio was expected, but all gave an excess of recessives except one family which segregated in equal proportions. These progenies, on the whole, were reasonably consistent in their deviation from the expected ratio.

Similar progenies were tested with strain B^1 (Table 21) and it was found that the segregations were similar to those obtained when strain A was used. These segregations are compared in Table 22. Gene R_3 controls resistance to both strains A and B^1 and consequently similar segregations were obtained.

The families shown in Table 23 represent the 3rd-generation derivatives of triple hybrid 885(2) tested with strain B^2. One of the parent plants of each progeny was selected from families 1253, 1257, 1258, 1270 and 1271 of the previous generation contained in /

in Table 20, where the only gene involved was R_3. The results of the two generations are comparable but the deviations from standard Mendelian ratios are less pronounced in the 3rd generation material than in the 2nd.

The results of further tests are shown in Table 24, where R_3 types are crossed with recessive, with R_1 and with R_2 types. Since both genes (R_3 and R_1) confer resistance to strain C they give a 3:1 ratio when intercrossed. $R_3 \times R_2$, on the other hand, gives a 1:1 ratio when tested with strain E because only the R_2 gene is effective against this strain.

TABLE 24.

DERIVATIVES OF TRIPLE HYBRIDS 885(2). GENE R_3.

REF. NO.	PARENTAGE	STRAIN	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1929abc	1253a(12) x A1695	C	102	156	0.65:1	1:1	R_3xr
1925a-d	1253a(12) x Aquila	C	97	45	2.16:1	3:1	R_3xR_1
1926ab	1253a(12) x Jakobi	C	182	72	2.53:1	3:1	R_3xR_1
1682c	1253a(12) x 1318(3)	E	38	42	0.90:1	1:1	R_3xR_2
1688d	1270b(9) x 910a(123)	A	70	69	1.01:1	1:1	R_3xr
1255d	Craigs Defiance x 997a(51)	C	100	107	0.93:1	1:1	rxR_3
1102c	885(2) x Cardinal	C	84	26	3.23:1	3:1	R_1R_3xr

The results of the double test (Table 25) show that

where /

where only the R_3 gene is present, the survivors of the C strain remain unaffected by strain B^2 since R_3 confers resistance to both strains and the progeny consists only of R_3 types and recessives. In the case of R_3 x R_1, however, where the seedlings segregate in the ratio of approximately 1 R_1R3 : 1 R_1 : 1 R_3 : 1 r, the C strain kills only the recessives but the B^2 strain kills the R_1 types. The survivors (50 per cent.) consist of R_1R_3 and R_3 types.

TABLE 25.

DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B^2).

REF. NO.	PARENTAGE		KILLED BY C	KILLED BY B^2	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1929c	1253a(12) x A1695	O	53	..	37	R_3 x r
		E	45	..	45	
1925cd	do. x Aquila	O	15	7	20	R_3 x R_1
		E	10.5	10.5	21	
1926b	do. x Jakobi	O	38	36	54	R_3 x R_1
		E	32	32	64	

O = observed. E = expected.

The resistant parent plants, 1253a(12), 1270b(9) and 997a(51), each possessing the gene R_3, were bred from triple hybrid 885(2). This triple hybrid, when crossed with Cardinal, gives a 3:1 ratio on testing with strain C (Table 24), and must therefore have two genes effective against this strain. As shown in Table 19, it contains two genes conferring resistance to strain A but only one to strain B^1. One of the genes has already been identified as R_3. The other must be R_1 to meet these requirements. /

requirements. Incidentally all plants possessing only the R_1 gene in the original progeny would be killed off in the B^1 strain test (Table 19). Triple hybrid 885(2) is thus represented by R_1R_3.

Triple Hybrid 885(3).

This triple hybrid was lost at an early stage in the experiments on account of the tubers rotting in storage and the three genes which the original tests with strains A and B^1 revealed (Table 19) could not all be identified. The surviving derivatives used as parents however, were all found to possess gene R_3.

2nd-generation derivatives of triple hybrid 885(3) are shown in Table 26, the progenies being tested with strain A. With one exception the segregation ratios showed an excess of recessive individuals compared with standard Mendelian ratios. The female parents of progenies 1323, 1324 and 1325 were derived from multiple hybrid W.800(2) which possesses gene R_1 only.

TABLE 26. /

TABLE 26.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3)

TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEOR-ETICAL	GENOTYPES (SIGNIFI-CANT TERMS ONLY)
1299	998a(7) ϕ N.S.	64	28	2.29:1	3:1	R_3
1300	998a(18) ϕ N.S.	36	14	2.57:1	3:1	R_3
1301	998a(43) ϕ N.S.	109	38	2.87:1	3:1	R_3
1302	998c(10) ϕ N.S.	194	68	2.85:1	3:1	R_3
		403	148	2.72:1	3:1	
1319	Craigs Defiance x 998a(7) ϕ	96	75	1.28:1	1:1)	r x R_3
1322	Ninetyfold x do.	68	81	0.84:1	1:1)	
		164	156	1.05:1	1:1	
1323	833a(25)⁎ x 998a(7)ϕ	111	43	2.58:1	3:1)	R_1 x R_3
1324	834b(6)⁎ x do.	265	84	3.15:1	3:1)	
1325	835a(4)⁎ x do.	80	32	2.50:1	3:1)	
		456	159	2.87:1	3:1	
1256	Craigs Defiance x 998a(18)ϕ	281	313	0.90:1	1:1)	
1265	Golden Wonder x do.	99	98	1.01:1	1:1)	r x R_3
1276	Southesk x do.	327	361	0.91:1	1:1)	
		707	772	0.92:1	1:1	
1327	E.P.C.106 x 998a(43)ϕ	70	103	0.68:1	1:1)	r x R_3
1328	E.P.C. 210 x do.	56	62	0.90:1	1:1)	
		126	165	0.76:1	1:1	

⁎ = Resistant to A strain. Susceptible to B^1 strain.

ϕ = Resistant to both A and B^1 strains.

N.S. = Natural Self.

833a(25), 834b(6), and 835a(4) were selected from progenies 833-5 quoted in Table 3.

E.P.C. 106 and E.P.C. 210 are varieties of S. andigenum.

In /

In Table 27 are shown the results of testing similar 2nd-generation derivatives of triple hybrid 885(3) with strain B^1. The segregations obtained are similar to those resulting from strain A because gene R_3 controls resistance to both strains. These results are compared in Table 28.

TABLE 27.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3) TESTED WITH STRAIN B^1.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
(1299) (1525)	998a(7) N.S.	215	56	3.84:1	3:1	R_3
1493	791a(116) x 998a(7)	45	57	0.79:1	1:1	r x R_3
1324	834b(6)* x do.	85	63	1.35:1	1:1	R_1 x R_3
		130	120	1.08:1	1:1	
1622	998a(18) N.S.	190	67	2.84:1	3:1	R_3
1494	791a(116) x 998a(18)	72	103	0.70:1	1:1)	r x R_3
1499	831(113) x do.	59	69	0.86:1	1:1)	
		131	172	0.76:1	1:1	

* = Resistant to A strain but susceptible to B^1 strain (Table 3).
N.S. = Natural Self.

TABLE 28. /

TABLE 28.

COMPARISON OF SEGREGATIONS IN STRAIN A AND STRAIN B^1 TESTS.

PARENTAGE	A STRAIN			B^1 STRAIN		
	SEEDLINGS TESTED	RATIO OBSERVED	RATIO THEORETICAL	SEEDLINGS TESTED	RATIO OBSERVED	RATIO THEORETICAL
998a(7) Selfed	92	2.29:1	3:1	271	3.84:1	3:1
Susceptible x 998a(7)	320	1.05:1	1:1	250	1.08:1	1:1
998a(18) Selfed	50	2.57:1	3:1	257	2.84:1	3:1
Susceptible x 998a(18)	1479	0.92:1	1:1	303	0.76:1	1:1

The segregations observed in 3rd-generation derivatives of triple hybrid 885(3) tested with strain B^1 are shown in Table 29. The resistant parent plants were selected from 2nd-generation progenies 1256 and 1276 shown in Table 26. The segregations in these two generations are similar.

The constitution of triple hybrid 885(3) is represented by $R_3R?R?$ since two genes cannot now be identified.

TABLE 29. /

TABLE 29.

3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3) TESTED WITH STRAIN B[1].

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1600ab	1256a(23) x Katahdin	119	130	0.91:1	1:1	R_3 x r
1601	1256a(23) x 910a(123)	32	39	0.82:1	1:1	
		151	169	0.89:1	1:1	
G911a	1276a(1) x Shamrock	26	48	0.54:1	1:1	
G912b	do.(4) x do.	73	84	0.87:1	1:1	
G886a	do.(12) x do.	49	49	1.0:1	1:1	R3 x r
1441	1276b(6) x 910a(123)	69	56	1.23:1	1:1	
G889	1276b(10) x Shamrock	42	43	0.98:1	1:1	
		259	280	0.93:1	1:1	

Triple Hybrid 885(4).

The segregations observed in 2nd-generation derivatives of triple hybrid 885(4) tested with strain A are included in Table 30.

TABLE 30. /

TABLE 30.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4)

TESTED WITH STRAIN A.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEOR-ETICAL	GENOTYPES (SIGNIFI-CANT TERMS ONLY)
1306	1104a(3) ø N.S.	134	12	11.17:1	15:1	R_3R_4
1332	1104a(6) ø N.S.	190	20	9.50:1	15:1	R_1R_3 or R_3R_4
		324	32	10.13:1	15:1	
1307	1104a(16) ø N.S.	124	44	2.82:1	3:1	R_3
1308	1104a(23) ø N.S.	23	8	2.88:1	3:1	R_3
		147	52	2.83:1	3:1	
1317	Epicure x 1104b(19)ø	151	253	0.60:1	1:1	r x R_3
1320	Craigs Defiance x 1104b(19)ø	38	58	0.66:1	1:1	
		189	311	0.61:1	1:1	

N.S. = Natural Self.
ø - Resistant to both A and B^1 strains.

From the figures obtained, it is apparent that 1104a(3) and 1104a(6) have two resistance genes in their constitution, while 1104a(16), 1104a(23) and 1104b(19) have only one. Derivatives of 1104a(3) and a sister plant 1104c(2) were tested with strain B^1 (Table 31) and gave segregations indicating the presence of two genes conferring resistance to this strain. When strain B^2 was used for testing comparable progenies (Table 32), the observed segregations were different in character and indicated the presence of only one effective gene in relation to strain B^2. The data in the two Tables are summarised and compared in Table 33. /

Table 33.

TABLE 31.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN B^1.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1528c	1104a(3) N.S.	208	15	13.87:1	15:1	R_3R_4
1488ab	Craigs Defiance x 1104a(3)	343	132	2.60:1	3:1	r x R_3R_4
1496a	791a(116) x 1104a(3)	142	62	2.29:1	3:1	
		485	194	2.50:1	3:1	
1503ab	835a(4)* x 1104a(3)	322	139	2.32:1	3:1	R_1 x R_3R_4
1518abc	882(5)ø x 1104a(3)	502	80	6.28:1	7:1	R_1R_2 x R_3R_4
1489	Craigs Defiance x 1104c(2)	158	49	3.22:1	3:1	r x R_3R_4
1497a	791a(116) x 1104c(2)	145	58	2.50:1	3:1	
		303	107	2.83:1	3:1	
1505ab	835a(4)* x 1104c(2)	339	196	1.73:1	3:1	R_1 x R_3R_4
1521ab	882(5)ø x 1104c(2)	469	77	6.09:1	7:1	R_1R_2 x R_3R_4

* = Resistant to A strain but susceptible to B^1 strain (Table 3).

ø = Resistant to both A and B^1 strains (see Table 49).

N.S. = Natural Self.

TABLE 32. /

TABLE 32.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN B^2.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1528b	1104a(3) N.S.	228	65	3.51:1	3:1	R_3R_4
1563ab	Craigs Defiance x 1104a(3)	280	246	1.14:1	1:1)	
1567a	Epicure x do.	131	120	1.09:1	1:1)	
1583ab	Southesk x do.	332	329	1.01:1	1:1)	r x R_3R_4
1591a	791a(116) x do.	132	97	1.36:1	1:1)	
1496b	do. x do.	82	67	1.22:1	1:1)	
		957	859	1.11:1	1:1	
1504ac	835a(4)⋇ x 1104a(3)	305	288	1.06:1	1:1	R_1 x R_3R_4
1518d	882(5)ø x 1104a(3)	116	37	3.14:1	3:1	R_1R_2 x R_3R_4
1624a	1104c(2) N.S.	156	59	2.64:1	3:1	R_3R_4
1564ab	Craigs Defiance x 1104c(2)	276	301	0.92:1	1:1)	
1572a	Gladstone x do.	188	184	1.02:1	1:1)	r x R_3R_4
1584ab	Southesk x do.	340	384	0.89:1	1:1)	
		804	869	0.93:1	1:1	
1506a	835a(4)⋇ x 1104c(2)	47	38	1.24:1	1:1)	R_1 x R_3R_4
1589abc	655(43)⋇ x do.	99	82	1.21:1	1:1)	
		146	120	1.22:1	1:1	
1521c	882(5)ø x 1104c(2)	194	66	2.94:1	3:1)	R_1R_2 x R_3R_4
1522a	do. x do.	162	70	2.31:1	3:1)	
		356	136	2.62:1	3:1	

⋇ = Resistant to A strain but susceptible to B^1 strain (Tables 3 and 4).
ø = Resistant to both A and B strains (see Table 49).
N.S. = Natural Self.

TABLE 33.

COMPARISON OF SEGREGATIONS IN TESTS WITH STRAINS B^1 AND B^2.

PARENTAGE	STRAIN B^1			STRAIN B^2		
	SEEDLINGS TESTED	RATIO OBSERVED	RATIO THEORETICAL	SEEDLINGS TESTED	RATIO OBSERVED	RATIO THEORETICAL
1104a(3) Selfed	223	13.87:1	15:1	293	3.51:1	3:1
Recessive x 1104a(3)	679	2.50:1	3:1	1816	1.11:1	1:1
R_1 x do.	461	2.32:1	3:1	593	1.06:1	1:1
R_1R_2 x do.	582	6.28:1	7:1	153	3.14:1	3:1
1104c(2) Selfed	..	..	15:1	215	2.64:1	3:1
Recessive x 1104c(2)	410	2.83:1	3:1	1673	0.93:1	1:1
R_1 x do.	535	1.73:1	3:1	266	1.21:1	1:1
R_1R2 x do.	546	6.09:1	7:1	492	2.62:1	3:1

Obviously 1104a(3) and 1104c(2) possess a gene which confers resistance to strain B^1 but is ineffective against strain B^2.

Some of the plants which proved resistant to strain B^1 (Table 31) were later attacked in the field by strain D. Critical tests carried out on them the following season showed that they were resistant to strains A, B^1 and E, but susceptible to B^2, C, D and F. These reactions revealed the presence of a new gene which has been designated R_4. Other segregates which were unaffected in the field by strain D proved to be resistant to strains A, B^1, B^2, C, D, G and H and susceptible to E, F and I. These are the reactions induced by gene R_3, and consequently the constitution /

constitution of 1104a(3) and 1104c(2) is represented by R_3R_4.

In order to confirm that the mode of transmission of gene R_4 is similar to that of the other R genes, two seedlings, 1506b and 1786a, were crossed with the recessive variety 11-79 and the resulting progenies (2160c and 2186c) tested with strain G. The segregations observed were 109 resistants : 112 susceptibles in family 2160c and 69 resistants : 71 susceptibles in family 2186c. These are close approximations to the expected 1:1 ratio and indicate that the mode of inheritance of R_4 is similar to that of R_1, R_2 and R_3.

Additional segregations in progenies bred from 1104a(3) and 1104c(2) are contained in Table 34.

TABLE 34. /

TABLE 34.

2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4).

GENES R_3 AND R_4.

REF. NO.	PARENTAGE	STRAIN	NO. OF SEEDLINGS R	NO. OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1495	791a(116) x 1104a(3)	A	81	40	2.03:1	3:1	r x R_3R_4
1568b	Epicure x 1104c(2)	A	123	41	3.00:1	3:1	r x R_3R_4
1810b	30-71 x 1104c(2)	C	56	57	0.98:1	1:1	r x R_3R_4
1563c	Craigs Defiance x 1104a(3)	E	153	159	0.96:1	1:1	
1567b	Epicure x do.	E	75	81	0.93:1	1:1	
1577	Majestic x do.	E	134	127	1.06:1	1:1	r x R_3R_4
1583c	Southesk x do.	E	160	143	1.12:1	1:1	
1591bc	791a(116)x do.	E	200	182	1.10:1	1:1	
			722	692	1.04:1	1:1	
1822a	1104a(3) Selfed	E	97	46	2.11:1	3:1	R_3R_4
1564c	Craigs Defiance x 1104c(2)	E	144	152	0.95:1	1:1	
1568a	Epicure x do.	E	129	120	1.08:1	1:1	
1584c	Southesk x do.	E	195	157	1.24:1	1:1	r x R_3R_4
1803	21-4 x do.	E	88	98	0.90:1	1:1	
1808a	24-15 x do.	E	57	37	1.54:1	1:1	
1809a) 1810a)	30-71 x do.	E	126	114	1.11:1	1:1	
1812a	30-73 x do.	E	60	56	1.07:1	1:1	
			799	734	1.09:1	1:1	
1823b	1104c(2) Selfed	E	150	56	2.68:1	3:1	R_3R_4
1506b	835a(4) x 1104c(2)	E	110	118	0.93	1:1	R_1 x R_3R_4

Tests with strain A confirm the presence of two genes, and the tests with /

with strains C and E respectively show that only one gene is effective in each case. In the last progeny in Table 34, obtained by crossing an R_1 type with 1104c(2), only R_4 types are resistant to strain E and a 1:1 ratio results.

The constitution of 1104a(3) and 1104c(2) is confirmed by triple tests and double tests shown in Table 35. In the triple tests the progenies were inoculated with strains A, D and E in turn, and the results are in accordance with expectation in the segregation ratio $1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain A kills the recessives (25 per cent.), strain D the R_4 types (25 per cent.), strain E the R_3 types (25 per cent.) and only the R_3R_4 types (25 per cent.) remain alive.

In the double test strain E kills the recessives and the R_3 types (50 per cent.), strain C kills the R_4 types (25 per cent.), and only the R_3R_4 types (25 per cent.) survive. When the sequence is reversed, strain C kills the recessives and the R_4 types (50 per cent.), strain E kills the R_3 types (25 per cent.), and the R_3R_4 types (25 per cent.) again survive.

Since 1104a(3) and 1104c(2) were bred from 885(4) x S. tuberosum, it follows that triple hybrid 885(4) must possess genes, R_3 and R_4. It was previously found, however (Table 19), that 885(4) had three genes conferring resistance to strain A, two of which were effective against strain B^1, and consequently one gene remains to be identified. From the information contained in Tables 35 and 36 it will be seen that 885(4) possesses :- /

possesses :-

3 genes conferring resistance to strain A
2 genes " " " B^1
1 gene " " " B^2
2 genes " " " C
1 gene " " " E

TABLE 35.

DOUBLE AND TRIPLE TESTS.

REF. NO.	PARENTAGE		KILLED BY A	D	E	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1495	791a(116) x 1104a(3)	O	40	20	31	30	r x R_3R_4
		E	30.25	30.25	30.25	30.25	
1568b	Epicure x 1104c(2)	O	41	31	44	48	r x R_3R_4
		E	41	41	41	41	
			E	C			
1567b	Epicure x 1104a(3)	O	81	39		36	r x R_3R_4
		E	78	39		39	
1568a	Epicure x 1104c(2)	O	120	67		62	r x R_3R_4
		E	124.5	62.25		62.25	
1823b	1104c(2) Selfed	O	56	40		110	R_3R_4
		E	51.5	38.625		115.875	
		T	4	3		9	
			C	E			
1810b	30-71 x 1104c(2)	O	57	25		31	r x R_3R_4
		E	56.5	28.25		28.25	

O = observed. E = expected. T = theoretical.

TABLE 36.

DOUBLE TESTS OF PROGENIES DERIVED FROM TRIPLE HYBRID 885(4).

REF. NO.	PARENTAGE		KILLED BY B^2	KILLED BY E	SURVIVED	TOTAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1464bc	885(4) x 910a(123)	O	46	26	24	96	$R_1R_3R_4$ x r
		E	48	24	24	96	
		T	4	2	2	8	
			E	C			
1819a	885(4) Selfed	O	9	6	61	76	$R_1R_3R_4$
		E	19	3.56	53.44	76	
		T	16	3	45	64	

O = observed. E = expected. T = theoretical.

Genes R_3 and R_4 fulfil the requirements with respect to two genes conferring resistance to strains A and B^1, and one gene giving resistance to strains B^2, C and E. The third gene must therefore provide resistance to strains A and C, i.e. it must be gene R_1, and the constitution of 885(4) is therefore $R_1R_3R_4$. In critical tests 885(4) proved to be resistant to all available strains except F, a behaviour which fits exactly with that expected from the genotype $R_1R_3R_4$.

One /

One of the triple hybrids, viz. 886(1), proved to be resistant to all available strains except C. This plant produced, on crossing with a recessive, a family of 27 seedlings, of which 20 were resistant and 7 susceptible to strain A. This is a close approximation to a 3:1 ratio and indicates the presence of two genes. Since 886(1) is susceptible to C only, the two genes would appear to be R_2 and R_4. In order to confirm this constitution, the 20 seedlings which survived the A strain test were inoculated with strain B^2. Six of them proved to be susceptible. The remaining 14 plants were inoculated with strain C and, as expected, all proved to be susceptible. The genotype of 886(1) is therefore R_2R_4, and the segregation ratio $1R_2R_4 : 1R_2 : 1R_4 : 1r$ in which the A strain kills the recessives and the B^2 strain the R_4 types.

Originally the F_1 hybrid, 735, was believed to have four genes conferring resistance to strain A (Table 19). It has proved to be resistant to all strains, and four genes have now been identified in the material bred from it. Only two genes, R_1 and R_3, give resistance to strain C, and consequently a selfed progeny of 735 tested with strain C should segregate in the ratio of 15 resistants : 1 susceptible. Such a ratio was obtained (Table 37).

TABLE 37. /

TABLE 37.

PROGENY OF F_1 HYBRID 735 TESTED WITH STRAIN C.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS		RATIO		GENOTYPES (SIGNIFICANT TERMS ONLY)
		R	r	OBSERVED	EXPECTED	
1109	735 Selfed	59	4	14.75:1	15:1	$R_1R_2R_3R_4$

The F_1 hybrid may therefore be credited with the genes R_1, R2, R3 and R_4, and S. demissum (CPC2127) with the same genes in the homozygous condition. No indication has yet been observed of the presence of others.

In Table 38 are shown the segregations obtained after inoculation with strain B^2 in progenies representing the 3rd-generation derivatives of triple hybrid 885(4). Seedling 1306a(2) was selected from a selfed progeny of 1104a(3) previously discussed. In relation to strain B^2, 1306a(2) possesses only one effective gene, viz. R_3, but as will be seen later gene R_4 is also present. The majority of the progenies contained an excess of recessive segregates compared with the theoretical ratios.

A number of offspring of 1104a(3) and 1104c(2) which behaved in the same manner towards the various strains were used as female parents in crosses with recessives and with Aquila (gene R_1). The progenies represent the 3rd-generation from triple hybrid 885(4). The constitution of the /

TABLE 38.

3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4)

TESTED WITH STRAIN B^2.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1630	1306a(2) N.S.	147	54	2.72:1	3:1	R_3R_4
1565	Craigs Defiance x 1306a(2)	54	65	0.83:1	1:1	
1569	Epicure x do.	144	162	0.89:1	1:1	
1573	Gladstone x do.	159	160	0.99:1	1:1	
1576	Kerr's Pink x do.	32	80	0.40:1	1:1	
1580	Majestic x do.	42	67	0.63:1	1:1	r x R_3R_4
1582	Ninetyfold x do.	35	38	0.92:1	1:1	
1592	791a(116) x do.	234	262	0.89:1	1:1	
1594	831(113) x do.	130	174	0.75:1	1:1	
1654	do. x do.	86	102	0.84:1	1:1	
1610	1-106 x do.	116	106	1.09:1	1:1	
1611	2-349 x do.	111	109	1.02:1	1:1	
		1143	1325	0.86:1	1:1	
1590	655(43)* x 1306a(2)	129	163	0.79:1	1:1	
1656-7	835a(4)* x do.	91	80	1.14:1	1:1	R_1 x R_3R_4
1613	Falke* x do.	87	115	0.76:1	1:1	
1618	Robusta* x do.	96	96	1.00:1	1:1	
		403	454	0.89:1	1:1	
1681	1253a(12)ø x 1306a(2)	292	114	2.56:1	3:1	
1598	1253a(15)ø x do.	249	70	3.56:1	3:1	R_3 x R_3R_4
1689	1270b(9)ø x do.	245	88	2.78:1	3:1	
1693	1271b(9)ø x do.	87	31	2.81:1	3:1	
		873	303	2.88:1	3:1	

* = Resistant to A strain but susceptible to B^2 strain.

ø = Resistant to both A and B^2 strains (see Table 23).

N.S. = Natural Self.

the female parents is the same throughout (R_3R_4), as shown in Table 39 where the C strain was employed for test purposes. In crosses with recessive pollen parents only the R_3 gene is effective and segregations of approximately 1:1 are obtained. In crosses with Aquila, however, in which gene R_1 is also effective, the ratios obtained approximate 3:1.

TABLE 39.
—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN C

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1964*a*	1564*a*(9) × Sickingen	87	106	0·82 : 1	1 : 1	$R_3R_4 \times r$
1965*a*	do. × 910*a*(123)	62	68	0·91 : 1	1 : 1	
1970*ab*	1567*a*(7) × 11–79	166	158	1·05 : 1	1 : 1	
1976*abc*	1591*a*(19) × 11–79	155	217	0·71 : 1	1 : 1	
		470	549	0·86 : 1	1 : 1	
1933*ab*	1488*b*(1) × Aquila	32	12	2·67 : 1	3 : 1	$R_3R_4 \times R_1$
1967	1564*a*(12) × do.	49	15	3·27 : 1	3 : 1	
1971*bc*	1584*b*(7) × do.	116	37	3·14 : 1	3 : 1	
1974*abc*	1591*a*(19) × do.	46	24	1·92 : 1	3 : 1	
		243	88	2·76 : 1	3 : 1	

Similar progenies were employed in a double test (Table 40), in which strain C was followed by strain E. Where a recessive was used as pollen parent the segregation ratio is $1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain C kills the recessives and the R_4 types (50 per cent.), strain E kills the R_3 types, and the R_3R_4 types survive. With Aquila as pollen parent, however, the ratio is $1R_1R_3R_4 : 1R_3R_4 : 1R_1R_3 : 1R_3 : 1R_1R_4 : 1R_4 : 1R_1 : 1r$. Strain C kills the recessive and R_4 types (25 per cent.), strain E kills the R_1, R_3 and R_1R_3 types (37.5 per cent.), and the remainder (37.5 per cent.) survive.

TABLE 40. /

TABLE 40.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by C	Killed by E	Survived	Genotypes (Significant Terms only)
1964*a*	1564*a*(9) × Sickingen	O	106	31	56	
		E	96·5	48·25	48·25	
1965*a*	do. × 910*a*(123)	O	68	33	29	
		E	65	32·5	32·5	
1970*ab*	1567*a*(7) × 11–79	O	158	75	91	$R_3R_4 \times r$
		E	162	81	81	
1976*ab*	1591*a*(19) × do.	O	159	44	63	
		E	133	66·5	66·5	
1933*ab*	1488*b*(1) × Aquila	O	12	19	13	
		E	11	16·5	16·5	
1967	1564*a*(12) × do.	O	15	29	20	
		E	16	24	24	$R_3R_4 \times R_1$
1971*bc*	1584*b*(7) × do.	O	37	52	64	
		E	38·25	57·375	57·375	
			C	B^2		
1976*c*	1591*a*(19) × 11–79	O	58	..	48	$R_3R_4 \times r$
		E	53	..	53	
1974*abc*	1591*a*(19) × Aquila	O	24	12	34	$R_3R_4 \times R_1$
		E	17·5	17·5	35	

O = observed. E = expected.

When strain C is followed by strain B^2, the latter has no effect on the C resisters in progenies derived from a recessive pollen parent, due to the presence of the R_3 gene. Where Aquila is pollen parent, however, strain C kills the recessive and the R_4 types (25 per cent.), strain B^2 kills the R_1 and R_1R_4 types (25 per cent.), and the $R_1R_3R_4$, R_3R_4, R_1R_3 and R_3 types (50 per cent.) survive.

Several seedlings bred from 1104a(3) and 1104c(2) crossed with recessives were used as female parents in crosses with 1318(3) (gene R_2) and the segregations are shown in Table 41. Seedlings 1563a(5) and 1563a(6) were susceptible to strain E, due to the absence of gene R_4, while seedlings 1563b(8) and 1564a(9) were resistant to all available strains except F due to the presence of both genes R_3 and R_4. The segregations obtained in /

in relation to the strains employed are in accordance with expectations.

TABLE 41.

3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) CROSSED WITH R_2 TYPE.

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1959*a*	1563*a*(5) × 1318(3)	E	46	56	0·82 : 1	1 : 1	$R_3 \times R_2$
1960*ab*	1563*a*(6) × do.	B^2	117	32	3·66 : 1	3 : 1	$R_3 \times R_2$
1962*a*	1563*b*(8) × do.	E	82	30	2·73 : 1	3 : 1	$R_3R_4 \times R_2$
1966*a–d*	1564*a*(9) × do.	C	182	225	0·81 : 1	1 : 1	$R_3R_4 \times R_2$

Similar progenies were submitted to double and triple tests and the results are shown in Table 42. The progenies derived from R_3R_4 x R_2 segregate according to the ratio $1R_2R_3R_4 : 1R_2R_3 : 1R_2R_4 : 1R_2 : 1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain C kills the recessives, R_2, R_4 and R_2R_4 types (50 per cent.), strain E kills the R_3 types (12.5 per cent.), and the remainder (37.5 per cent.) survive. When strain F is used instead of E for the second part of the test, it kills the R_3 and R_3R_4 types (25 per cent.) and only 25 per cent. survive.

The segregation in the progenies derived from R_3 x R_2 is represented by the ratio $1R_2R_3 : 1R_2 : 1R_3 : 1r$. The E strain kills the recessives and R_3 types (50 per cent.), the F strain is ineffective against the remainder, but the C strain kills the R_2 types (25 per cent.) and only the R_2R_3 types (25 per cent.) survive. In the last case strain B^2 kills the recessives (25 per cent.), F kills the R_3 types (25 per cent.), C kills the R_2 types (25 per cent.), and again the only survivors are /

are the R_2R_3 types (25 per cent.).

TABLE 42.

DOUBLE AND TRIPLE TESTS.

Ref. No.	Parentage		Killed by			Survived	Genotypes (Significant Terms only)
			C	E			
1966*a*	1564*a*(9) × 1318(3)	O	76	13		51	$R_3R_4 \times R_2$
		E	70	17·5		52·5	
			C	F			
1966*b*	1564*a*(9) × 1318(3)	O	72	30		25	$R_3R_4 \times R_2$
		E	63·5	31·75		31·75	
			E	F	C		
1959*a*	1563*a*(5) × 1318(3)	O	56	..	21	25	$R_3 \times R_2$
		E	51	..	25·5	25·5	
			B^2	F	C		
1960*ab*	1563*a*(6) × 1318(3)	O	32	35	39	43	$R_3 \times R_2$
		E	37·25	37·25	37·25	37·25	

O = observed. E = expected.

Two seedlings, 1306a(2) and 1306a(15), obtained by selfing 1104a(3) (Table 30), were employed as parents in crosses with recessive types and the results are shown in Table 43. Various progenies bred from 1306a(2) were previously examined in B^2 strain tests (Table 38).

TABLE 43. /

TABLE 43.

3RD- AND 4TH-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) (1306a(2), 1306a(15) AND 1439a(4)).

Ref. No.	Parentage		Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1574*a*	Gladstone	× 1306*a*(2)	B^2+C	34	43	0·79 : 1	1 : 1	$r \times R_3R_4$
1610*b*	1–106	× do.	E	65	70	0·93 : 1	1 : 1	
1431*a*	Arran Victory	× 1306*a*(15)	B^1	108	17	6·35 : 1	7 : 1	
1433*abc*	Craigs Defiance	× do.	B^1	354	37	9·57 : 1	7 : 1	
1434*a*	do.	× do.	B^1	75	10	7·50 : 1	7 : 1	
1436	Gladstone	× do.	B^1	141	9	15·67 : 1	7 : 1	$r \times R_3R_3R_4$
1437*abc*	Majestic	× do.	B^1	406	52	7·81 : 1	7 : 1	
1438	Southesk	× do.	B^1	177	12	14·75 : 1	7 : 1	
1439*ab*	do.	× do.	B^1	178	23	7·74 : 1	7 : 1	
				1439	160	8·99 : 1	7 : 1	
1799	1439*a*(4)	× Flava	C	95	99	0·96 : 1	1 : 1	$R_3 \times r$
1800*a*	do.	× 834*c*(29)	C	80	41	1·95 : 1	3 : 1	$R_3 \times R_1$

From these results and the evidence set out in Tables 43 and 44 it is apparent that 1306a(2) possesses :-

2 genes conferring resistance to strain A

1 gene " " " B^2

1 " " " " C

1 " " " " E

The genes may thus be identified as R_3R_4, the same constitution as 1104a(3) from which 1306a(2) was bred.

The segregations obtained from 1306a(15), although slightly inconsistent, are characterised by an unexpectedly high proportion of resistant plants (Table 43). The average in tests with strain B^1, shows a ratio of 8.99 : 1, but if this b regarded /

regarded as a theoretical 7 : 1 ratio, then the constitution of 1306a(15) may be deduced from the results of the double tests shown in Table 44. The available information indicates that 1306a(15) possesses :-

3 genes conferring resistance to strain A
3 " " " " B^1
2 " " " " B^2
2 " " " " C
1 gene " " " E

Since it was bred from 1104a(3) only R_3 and R_4 genes can be present, and the constitution of $R_3R_3R_4$ is the only one which fits. Such a genotype might be expected to exhibit some irregularity in segregations because of the presence of two R_3 genes and the relative affinity of the chromosomes carrying them. Consistent pairing of these homologues would of course produce only resistant offspring, but a relatively greater affinity at meiosis would merely tend to increase the proportion of resistant seedlings and give ratios such as those observed in Tables 43 and 44.

TABLE 44.

DOUBLE AND QUADRUPLE TESTS.

Ref. No.	Parentage		Killed by A	C	B^2	E	Survived	Total	Genotypes (Significant Terms only)
1824*b*	1306*a*(2) Selfed	O	10	22	..	23	53	108	R_3R_4
		E	6·75	20·25	..	20·25	60·75	108	
		T	1	3	..	3	9	16	
			A		B^2				
1433*d*	Craigs Defiance × 1306*a*(15)	O	11		6		65	82	$r \times R_3R_3R_4$
		E	10·25		10·25		61·5	82	
		T	1		1		6	8	
				C		E			
1431*b*	Arran Victory × 1306*a*(15)	O		23		54	40	117	$r \times R_3R_3R_4$
		E		29·25		43·875	43·875	117	
		T		2		3	3	8	

O = observed. E = expected. T = theoretical.

A seedling, 1439a(4), bred from Southesk x 1306a(15) was crossed with a recessive and an R_1 type and gave 1 : 1 and 3 : 1 ratios respectively when tested with strain C (Table 43). Since 1439a(4) is susceptible to strain E, the R_4 gene must be absent and its constitution is accordingly represented by R_3.

Another seedling, 1307a(23), which was obtained by selfing 1104a(16) (Table 30), also gave abnormal segregation ratios. It was found to be resistant to strains A, B^1, B^2, C and D and susceptible to E and F, a series of reactions typical of those of R_3 plants. Since the parent plant 1104a(16) had only one gene, the offspring 1307a(23) may be represented by R_3R_3.

In Table 45 progeny tests of 1307a(23) are set out in three groups, viz. recessive x 1307a(23), R_3 types x 1307a(23) and 1307a(23) selfed. The R_3 types in the second group were members of progenies previously examined (Tables 20 and 26). The outstanding feature of all progenies is the large and consistent excess of resistant segregates compared with the theoretical ratios. Since 1307a(23) can have inherited not more than two genes, it is concluded that the high proportion of resistant seedlings observed is due to a greater affinity of the R_3-bearing chromosomes for each other than for their alternative allelomorphs which probably had different specific origin. The figures indicate that the chromosomes carrying the R_3 genes paired with each other almost as frequently as they did with the alternative allelomorphs which would be their normal /

normal partners if allo-syndesis prevailed. Apparently auto-syndesis and allo-syndesis occurred in approximately equal proportions in this tetraploid plant, giving ratios characteristic of autotetraploids.

TABLE 45.

3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) (1307a(23)).

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1566*a*	Craigs Defiance × 1307*a*(23)	B^2	117	16	7·31 : 1	3 : 1	$r \times R_3R_3$
1566*bc*	do. × do.	C	141	15	9·40 : 1	3 : 1	
1570*ab*	Epicure × do.	B^2	78	13	6·00 : 1	3 : 1	
1575	Gladstone × do.	B^2	175	20	8·75 : 1	3 : 1	
1593*ab*	791*a*(116) × do.	B^2	222	30	7·40 : 1	3 : 1	
			733	94	7·80 : 1	3 : 1	
1599*ab*	1253*a*(15) × 1307*a*(23)	B^2	96	6	16·00 : 1	7 : 1	$R_3 \times R_3R_3$
1602*ab*	1256*a*(23) × do.	B^2	212	13	16·31 : 1	7 : 1	
1606	1258*a*(19) × do.	B^2	64	10	6·40 : 1	7 : 1	
			372	29	12·83 : 1	7 : 1	
1631*ab*	1307*a*(23) Selfed	A	146	5	29·20 : 1	15 : 1	R_3R_3
1527*abc*	do.	B^1	231	10	23·10 : 1	15 : 1	
1631*c*, 1726*bc*	do.	B^2	200	5	40·00 : 1	15 : 1	
			577	20	28·85 : 1	15 : 1	

Seedling progenies, obtained by crossing triple hybrid derivatives with the R_2 types, 1318(3) and 1315b(10), were tested with strains B^2 and C as indicated in Table 46. The triple hybrid derivatives employed as parents, viz. 1253a(12), 1270b(9), 1271b(11), were previously credited with gene R_3 while 1306a(2) was found to possess genes R_3 and R_4.

The intercrossing of R_2 and R_3 genotypes gives progenies which segregate in the ratio of approximately 3 resistants : 1 susceptible when tested with strain B^2, and approximately /

approximately in equal proportions when tested with strain C. These results would be expected since both parents are B^2 resistant but only one of them is C resistant.

TABLE 46.

DERIVATIVES OF 877a(34) and TRIPLE HYBRIDS

TESTED WITH STRAINS B^2 and C.

REF. NO.	PARENTAGE	STRAIN	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1682ab	1253a(12) x 1318(3)	B^2	109	35	3.11:1	3:1	$R_3 \times R_2$
1691a	1270b(9) x do.	B^2	140	44	3.18:1	3:1	$R_3 \times R_2$
1696	1271b(11) x do.	B^2	225	71	3.17:1	3:1	$R_3 \times R_2$
1698a	1315b(10) x 1306a(2)	B^2	111	43	2.58:1	3:1	$R_2 \times R_3R_4$
1699	do. x 1332a(6)	B^2	194	73	2.66:1	3:1	$R_2 \times R_3$
			779	266	2.93:1		
1691b	1270b(9) x 1318(3)	C	121	138	0.88:1	1:1	$R_3 \times R_2$
1698c	1315b(10) x 1306a(2)	C	82	102	0.80:1	1:1	$R_2 \times R_3R_4$
			203	240	0.85:1		

As shown in Table 47, approximately 25 per cent. of the individuals are killed by the B^2 strain. Subsequent inoculation of the survivors with strain C destroys approximately one-third of the B^2 resisters. When the C strain is used first, however, approximately half of the plants are killed by it (Table 48), and the remainder are unaffected by exposure to strain B^2.

TABLE 47. /

TABLE 47.

DOUBLE TEST (STRAIN B^2 FOLLOWED BY STRAIN C).

REF. NO.	PARENTAGE		KILLED BY B^2	KILLED BY C	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1691a	1270b(9) x 1318(3)	O	44	37	103	$R_3 \times R_2$
		E	46.0	46.0	92.0	
1696	1271b(11) x 1318(3)	O	71	70	155	$R_3 \times R_2$
		E	74.0	74.0	148.0	
1699	1315b(10) x 1332a(6)	O	73	68	126	$R_2 \times R_3$
		E	66.75	66.75	133.5	
1698a	1315b(10) x 1306a(2)	O	43	35	76	$R_2 \times R_3R_4$
		E	38.5	38.5	77.0	

O = observed. E = expected.

TABLE 48.

DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B^2).

REF. NO.	PARENTAGE		KILLED BY C	KILLED BY B^2	SURVIVED	GENOTYPES (SIGNIFICANT TERMS ONLY)
1691b	1270b(9) x 1318(3)	O	138	..	121	$R_3 \times R_2$
		E	129.5	..	129.5	
1698c	1315b(10) x 1306a(2)	O	102	..	82	$R_2 \times R_3R_4$
		E	92	..	92	

O = observed. E = expected.

This evidence indicates that the progenies segregate in the ratio of approximately $1R_2R_3 : 1R_2 : 1R_3 : 1r$. Strain B^2 can kill only the recessives (25 per cent.), while strain C is effective against the R_2 segregates (25 per cent.) as well as the recessives. In these progenies, therefore, the C strain alone gives the same results as would a mixture of the two strains B^2 and C, and the only plants /

plants which would survive would be those possessing the R_3 gene with or without the help of the R_2 gene.

Progenies Related to Hybrid 882(5).

Seedling 882(5), which has been widely employed as a female parent in breeding experiments, was bred from the original S. demissum-S. tuberosum material and its pedigree is detailed in Fig. 4. Although S. Rybinii also features in the pedigree, its employment as a parent was in this case not directly associated with S. demissum and may be regarded as incidental. The blight resistance of seedling 882(5) was inherited from 692a(52), a selection from family 692 (Table 17).

TABLE 49.

DERIVATIVES OF HYBRID 882(5) TESTED WITH STRAIN B^2.

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1508	882(5) x Katahdin	136	127	1.07:1	1:1	R_1R_2 x r
1509	do. x do.	113	129	0.88:1	1:1	
1510	do. x Dr McIntosh	69	78	0.88:1	1:1	
1511	do. x M233(13)	69	84	0.82:1	1:1	
1516	do. x 910a(123)	265	258	1.03:1	1:1	
1517	do. x do.	105	122	0.86:1	1:1	
1669	do. x do.	55	58	0.95:1	1:1	
1670	do. x do.	74	56	1.32:1	1:1	
		886	912	0.97:1	1:1	

1662 /

TABLE 49 (Contd.)

REF. NO.	PARENTAGE	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
1662	882(5) x 834b(6)	29	19	1.53:1	1:1	R_1R_2 x R_1
1663	do. x do.	68	42	1.62:1	1:1	
		97	61	1.59:1	1:1	
1512	882(5) x 834c(29)	360	355	1.01:1	1:1	
1513	do. x do.	219	238	0.92:1	1:1	
1514	do. x do.	109	129	0.84:1	1:1	
1515	do. x do.	72	86	0.84:1	1:1	R_1R_2 x R_1
1665	do. x do.	20	23	0.87:1	1:1	
1666	do. x do.	35	46	0.76:1	1:1	
1667	do. x do.	92	78	1.18:1	1:1	
		907	955	0.95:1	1:1	

Table 49 refers to the segregations in progenies bred from 882(5). In crosses with recessive and with R_1 types approximately equal proportions of resistants and susceptibles were obtained using strain B^2. This information, together with that set out in Tables 50 and 51 dealing with 882(5) crossed with recessives, demonstrates that 882(5) possesses :-

2 genes conferring resistance to strain A
1 gene " " " B^2
1 " " " " C
1 " " " " E
1 " " " " F

The genes present must therefore be R_1R_2.

When /

When R_1R_2 types are crossed with recessives the genotypic segregation is $1R_1R_2 : 1R_1 : 1R_2 : 1r$. The A strain can kill only the recessives and a 3 : 1 ratio results. Strain C kills the R_2 types as well as the recessives, giving a 1 : 1 ratio, while strain E kills the R_1 types and the recessives, giving also a 1 : 1 ratio.

In the double tests (Table 51) strain C kills the R_2 types ~~types~~ and the recessives (50 per cent.), strain F kills the R_1 types (25 per cent.), and the R_1R_2 types survive (25 per cent.). When strain E is substituted for F the same results are obtained. If the sequence is reversed, strain E followed by C, the recessives and R_1 types are killed by E, the R_2 types by C, and the R_1R_2 types survive as before.

TABLE 50.

5TH-GENERATION DERIVATIVES OF S. DEMISSUM X S. TUBEROSUM (882(5)).

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1508*b*, 1509*ab*	882(5) × Katahdin	A	271	98	2·77 : 1	3 : 1	$R_1R_2 \times r$
1511*b*	882(5) × M233(13)	C	64	58	1·10 : 1	1 : 1	
1914*a*	do. × Alness	C	58	85	0·68 : 1	1 : 1	
1915*ab*	do. × Gladstone	C	91	93	0·98 : 1	1 : 1	
1916*a*	do. × Sickingen	C	75	68	1·10 : 1	1 : 1	$R_1R_2 \times r$
1921*ab*	do. × 21–4	C	131	129	1·01 : 1	1 : 1	
1922*a*	do. × 23–22	C	43	37	1·16 : 1	1 : 1	
1923*a–j*	do. × 11–79	C	845	754	1·12 : 1	1 : 1	
			1307	1224	1·07 : 1	1 : 1	
1670*bd*	882(5) × 910*a*(123)	E	75	63	1·19 : 1	1 : 1	
1790*ab*	do. × Sickingen	E	99	96	1·03 : 1	1 : 1	$R_1R_2 \times r$
1791	do. × 21–4	E	46	54	0·85 : 1	1 : 1	
1792*ab*	do. × 23–22	E	82	86	0·95 : 1	1 : 1	
			302	299	1·01 : 1	1 : 1	

TABLE 51.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Genotypes (Significant Terms only)
1915*b*	882(5) × Gladstone	O	38	23	19	$R_1R_2 \times r$
		E	40	20	20	
1921*a*	do. × 21–4	O	57	37	41	$R_1R_2 \times r$
		E	67·5	33·75	33·75	
1922*a*	do. × 23–22	O	37	20	23	$R_1R_2 \times r$
		E	40	20	20	
1923*b–d g–j*	do. × 11–79	O	506	290	289	$R_1R_2 \times r$
		E	542·5	271·25	271·25	
			C	E		
1923*a*	882(5) × 11–79	O	82	44	51	$R_1R_2 \times r$
		E	88·5	44·25	44·25	
			E	C		
1670*bd*	882(5) × 910*a*(123)	O	63	30	45	$R_1R_2 \times r$
		E	69	34·5	34·5	

O = observed. E = expected.

882(5) was crossed with R_1 types (bred from multiple hybrid W.800(2)) and R_2 types (related to S. demissum-S. tuberosum hybrid 877a(34)), and the results are shown in Tables 52 and 53. In seedlings bred from R_1R_2 x R_1, the R_2 gene only is effective against strain E and a 1 : 1 ratio results. Progenies obtained from R_1R_2 x R_2 have two genes effective against strains B^2 and E and give 3 : 1 ratios, but only one gene is effective against C and 1 : 1 ratios result.

TABLE 52. /

TABLE 52.

PROGENIES DERIVED FROM 882(5) CROSSED WITH R_1 AND R_2 TYPES.

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1664*abc*	882(5) × 834*b*(6)	E	220	214	1·03 : 1	1 : 1	$R_1R_2 \times R_1$
1514*b*	do. × 834*c*(29)	E	78	86	0·91 : 1	1 : 1	
1668*abc*	do. × do.	E	206	226	0·91 : 1	1 : 1	
			504	526	0·96 : 1	1 : 1	
1671, 1672*a*	882(5) × 1318(3)	B^2	167	55	3·04 : 1	3 : 1	$R_1R_2 \times R_2$
1673*c*	882(5) × 1318(3)	C	46	46	1·00 : 1	1 : 1	$R_1R_2 \times R_2$
1972*b*	do. × do.	C	54	52	1·04 : 1	1 : 1	
1917*ab*	do. × 877*a*(34)	C	54	42	1·29 : 1	1 : 1	
			154	140	1·10 : 1	1 : 1	
1673*ab*	882(5) × 1318(3)	E	173	58	2·98 : 1	3 : 1	$R_1R_2 \times R_2$

TABLE 53.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by E	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1664*b*	882(5) × 834*b*(6)	O	63	17	45	125	$R_1R_2 \times R_1$
		E	62·5	15·625	46·875	125	
		T	4	1	3	8	
1668*c*	do. × 834*c*(29)	O	79	22	40	141	$R_1R_2 \times R_1$
		E	70·5	17·625	52·875	141	
		T	4	1	3	8	
			B^2	C			
1671	882(5) × 1318(3)	O	20	24	45	89	$R_1R_2 \times R_2$
		E	22·25	33·375	33·375	89	
		T	2	3	3	8	
			C	F			
1917*ab*	882(5) × 877*a*(34)	O	42	13	41	96	$R_1R_2 \times R_2$
		E	48	12	36	96	
		T	4	1	3	8	

O = observed. E = expected. T = theoretical.

R_1R_2 types x R_1 types segregate according to the genotypic ratio $1R_1R_1R_2 : 2R_1R_2 : 1R_2 : 1R_1R_1 : 2R_1 : 1r$. As shown in double tests (Table 53), the E strain kills 50 per cent., i.e. /

i.e. all segregates lacking R_2; of the remainder the C strain kills 12.5 per cent., i.e.those lacking R_1. The survivors, 37.5 per cent., have both genes in their constitution.

In the progenies obtained from R_1R_2 x R_2 the genotypic ratio is $1R_1R_2R_2 : 2R_1R_2 : 1R_1 : 1R_2R_2 : 2R_2 : 1r$. The B^2 strain kills 25 per cent., i.e. those lacking R_2, the C strain a further 37.5 per cent., i.e. those lacking R_1, and the survivors, 37.5 per cent., possess both genes. In the last progeny mentioned in Table 53 the C strain kills those lacking R_1 (50 per cent.), the F strain kills those lacking R_2 (a further 12.5 per cent.), and again the plants possessing both genes survive (37.5 per cent.).

Parent plants 1517b(2) and 1509a(4) (Table 54) bred from 882(5) x recessive were back-crossed to recessives. The results show that 1517b(2) has the same constitution as 882(5), viz. R_1R_2, and that the ratios obtained are in close agreement with those calculated on the basis of the genotypic ratio $1R_1R_2 : 1R_1 : 1R_2 : 1r$.

TABLE 54. /

TABLE 54.

DOUBLE TESTS OF PROGENIES DERIVED FROM (882(5) x RECESSIVE) X RECESSIVE.

Ref. No.	Parentage		Killed by C	Killed by E	Survived	Genotypes (Significant Terms only)
1951*a*	1517*b*(2) × 910*a*(123)	O	75	39	41	$R_1R_2 \times r$
		E	77·5	38·75	38·75	
1952*a*	do. × 23–22	O	59	22	29	$R_1R_2 \times r$
		E	55	27·5	27·5	
			C	F		
1951*b*	1517*b*(2) × 910*a*(123)	O	23	23	17	$R_1R_2 \times r$
		E	31·5	15·75	15·75	
1952*bcd*	do. × 23–22	O	206	117	103	$R_1R_2 \times r$
		E	213	106·5	106·5	
			F	C		
1940*a*	1509*a*(4) × 23–22	O	65	75	..	$R_2 \times r$
		E	70	70	..	

O = observed. E = expected.

In the case of 1509a(4), the F strain killed half of the progeny and the C strain killed the remainder. Obviously gene R_1 is absent from this plant and its constitution must be represented by R_2.

In Table 55 the parent plants 1508b(3), 1509a(3), 1517a(1) and 1517b(2), bred from 882(5) x recessive, were crossed with R_1 and R_3 types. 1517b(2) proved resistant to C & F strains, but the others were susceptible to strain C. The segregations observed show that 1508b(3), 1509a(3) and 1517a(1) are R_2 types and that 1517b(2) is represented by R_1R_2. In family 1949f a mixture of C and F strains were employed and the resulting segregation approached the theoretical 3 : 5 ratio.

TABLE 55. /

TABLE 55.

PROGENIES DERIVED FROM (882(5) x RECESSIVE) x R1 AND R3

TYPES.

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1898*ab*	835*a*(4) × 1508*b*(3)	C	76	105	0·72 : 1	1 : 1	$R_1 \times R_2$
1930*bc*	1439*a*(4) × 1508*b*(3)	C	111	123	0·90 : 1	1 : 1	$R_3 \times R_2$
1930*d*	do. × do.	F	41	39	1·05 : 1	1 : 1	
1899*acg*	853*a*(4) × 1509*a*(3)	C	187	209	0·89 : 1	1 : 1	$R_1 \times R_2$
1899*be*	do. × do.	F	118	142	0·83 : 1	1 : 1	
1943*a–k*	1517*a*(1) × Aquila	C	411	480	0·86 : 1	1 : 1	$R_2 \times R_1$
1944	do. × 914*a*(91)	C	49	59	0·83 : 1	1 : 1	
1948*a–g*, 1949*bcdj*	1517*b*(2) × Aquila	C	1365	464	2·94 : 1	3 : 1	$R_1R_2 \times R_1$
1949*ae*	do. × do.	F	165	159	1·04 : 1	1 : 1	
1949*f*	do. × do	C+F	84	92	4·57 : 5	3 : 5	
1950*ab*	do. × 834*c*(29)	C	73	29	2·52 : 1	3 : 1	

TABLE 56.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Total	Genotypes (Significant Terms only)
1898*ab*	835*a*(4) × 1508*b*(3)	O	105	41	35	181	$R_1 \times R_2$
		E	90·5	45·25	45·25	181	
1930*bc*	1439*a*(4) × do.	O	123	57	54	234	$R_3 \times R_2$
		E	117	58·5	58·5	234	
1899*ac*	835*a*(4) × 1509*a*(3)	O	134	66	62	262	$R_1 \times R_2$
		E	131	65·5	65·5	262	
1943*c–k*	1517*a*(1) × Aquila	O	325	128	137	590	$R_2 \times R_1$
		E	295	147·5	147·5	590	
1944	do. × 914*a*(91)	O	59	25	24	108	$R_2 \times R_1$
		E	54	27	27	108	
1948*cdfg*, 1949*bc*	1517*b*(2) × Aquila	O	225	361	345	931	$R_1R_2 \times R_1$
		E	232·75	349·125	349·125	931	
		T	2	3	3	8	
1950*ab*	do. × 834*c*(29)	O	29	30	43	102	$R_1R_2 \times R_1$
		E	25·5	38·25	38·25	102	
		T	2	3	3	8	
			F	C			
1930*d*	1439*a*(4) × 1508*b*(3)	O	39	22	19	80	$R_3 \times R_2$
		E	40	20	20	80	
1899*b*	835*a*(4) × 1509*a*(3)	O	58	29	23	110	$R_1 \times R_2$
		E	55	27·5	27·5	110	
1949*ae*	1517*b*(2) × Aquila	O	159	46	119	324	$R_1R_2 \times R_1$
		E	162	40·5	121·5	324	
		T	4	1	3	8	
			C	B^2			
1949*d*	1517*b*(2) × Aquila	O	51	66	83	200	$R_1R_2 \times R_1$
		E	50	75	75	200	
		T	2	3	3	8	
			C	E			
1948*a*	1517*b*(2) × Aquila	O	41	67	72	180	$R_1R_2 \times R_1$
		E	45	67·5	67·5	180	
		T	2	3	3	8	

O = observed. E = expected. T = theoretical.

The same or similar progenies were subjected to double tests as shown in Table 56. In crosses between R_1 types and R_2 types the C strain kills the recessives and the R_2 plants (50 per cent.), the F strain kills the R_1 plants (25 per cent.), and the R_1R_2 types (25 per cent.) survive. The same figures are obtained in R_3 x R_2 progenies because strains C and F have the same effect on R_3 as on R_1 genotypes. Where R_1R_2 types are crossed with R_1, the C strain kills the recessives and R_2 types (25 per cent.), the F strain kills the R_1 types (37.5 per cent.), and the survivors (37.5 per cent.) are those possessing both genes. When the sequence is reversed (F followed by C), the proportions killed in R_1 x R_2 families are the same as before, but in progenies obtained from R_1R_2 x R_1 the F strain kills 50 per cent., the C strain 12.5 per cent., and the same 37.5 per cent. survive. Table 56 also shows that if B^2 or E is substituted for F, the results remain exactly the same since B^2, E and F have the same effect on R_1 and on R_2 genotypes.

Seedling 1512c(14), bred from 882(5) (R_1R_2) x R_1 type (Table 49), was used as a pollen parent in a series of crosses (Table 57). Since it proved to be susceptible to strain F, strain C and resistant to ~~all the others,~~ it must possess only the gene R_2. That this is so is confirmed by the results of crosses with recessives, R_1, R_3 and R_3R_4 types shown in Table 57, and also by the results of the double and triple tests contained in /

in Table 58.

TABLE 57.

PROGENIES DERIVED FROM 1512c(14) (882(5) x R1 TYPE) CROSSED WITH RECESSIVE, R_1, R_3 AND R_3R_4 TYPES.

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1912*a*	Ulster Supreme × 1512*c*(14)	F	81	77	1·05 : 1	1 : 1	$r \times R_2$
1977*a*	24–15 × do.	E	100	90	1·11 : 1	1 : 1	
1900*bde*	835*a*(4) × 1512*c*(14)	C	155	192	0·81 : 1	1 : 1	$R_1 \times R_2$
1905*a*	Kennebec × do.	C	43	53	0·81 : 1	1 : 1	
1924*abc*	914*a*(12) × do.	C	193	205	0·94 : 1	1 : 1	
			391	450	0·87 : 1	1 : 1	
1900*f*	835*a*(4) × 1512*c*(14)	C+F	39	108	1·08 : 3	1 : 3	$R_1 \times R_2$
1928*abe*	1253*a*(12) × 1512*c*(14)	C	164	174	0·94 : 1	1 : 1	$R_3 \times R_2$
1928*fh*	do. × do.	F	111	114	0·97 : 1	1 : 1	
1931*abk*	1439*a*(4) × do.	C	380	401	0·95 : 1	1 : 1	
1934*a–d*	1488*b*(1) × 1512*c*(14)	C	215	225	0·96 : 1	1 : 1	$R_3R_4 \times R_2$
1980*a*	1512*c*(14) Selfed	E	114	38	3·00 : 1	3 : 1	R_2

TABLE 58. /

TABLE 58.

DOUBLE AND TRIPLE TESTS.

Ref. No.	Parentage		Killed by E	F	C	Survived	Genotypes (Significant Terms only)
1977*a*	24–15 × 1512*c*(14)	O	90	..	100	..	$r \times R_2$
		E	95	..	95	..	
			C	B^2	F		
1900*e*	835*a*(4) × 1512*c*(14)	O	44	22	..	24	$R_1 \times R_2$
		E	45	22·5	..	22·5	
			C	B^2			
1924*c*	914*a*(12) × 1512*c*(14)	O	64	37		34	$R_1 \times R_2$
		E	67·5	33·75		33·75	
1928*e*	1253*a*(12) × 1512*c*(14)	O	69	..		67	$R_3 \times R_2$
		E	68	..		68	
			C	E			
1934*a*	1488*b*(1) × 1512*c*(14)	O	73	21		51	$R_3R_4 \times R_2$
		E	72·5	18·125		54·375	
		T	4	1		3	
			C	F			
1905*a*	Kennebec × 1512*c*(14)	O	53	24		19	$R_1 \times R_2$
		E	48	24		24	
1924*ab*	914*a*(12) × 1512*c*(14)	O	141	68		54	$R_1 \times R_2$
		E	131·5	65·75		65·75	
1928*b*	1253*a*(12) × 1512*c*(14)	O	64	25		33	$R_3 \times R_2$
		E	61	30·5		30·5	
1931*ab*	1439*a*(4) × 1512*c*(14)	O	306	144		145	$R_3 \times R_2$
		E	297·5	148·75		148·75	
1934*bcd*	1488*b*(1) × 1512*c*(14)	O	152	79		64	$R_3R_4 \times R_2$
		E	147·5	73·75		73·75	
		T	4	2		2	
			F	C			
1928*f*	1253*a*(12) × 1512*c*(14)	O	47	24		25	$R_3 \times R_2$
		E	48	24		24	

O = observed. E = expected. T = theoretical.

Its practical value in crosses with recessives is doubtful, but in crosses with R_1, R_3 or R_3R_4 types, 25 per cent. of the seedlings in each case are resistant to both C and F strains. ~~all seven~~ R_1 x R_2 gives the segregation ratio $1R_1R_2 : 1R_1 : 1R_2 : 1r$ in which only the R_1R_2 types can survive the double test of strain C with either B^2, or E or F. In the case of R_3 x R_2 the /

the segregation ratio is $1R_2R_3 : 1R_2 : 1R_3 : 1r$, and strain C together with E or F kill all except the R_2R_3 types. If strain B^2 is used instead of E or F, the R_3 types also survive. $R_3R_4 \times R_2$ gives the segregation ratio $1R_2R_3R_4 : 1R_2R_3 : 1R_2R_4 : 1R_2 : 1R_3R_4 : 1R_3 : 1R_4 : 1r$. If strains C and E are used the survivors are the $R_2R_3R_4$, R_2R_3 and R_3R_4 types (37.5 per cent.), but if E is replaced by F the R_3R_4 type is also killed, and the proportion of survivors is reduced to 25 per cent.

A plant of similar origin, 1512d(4), proved to be resistant to both C and F strains, and when crossed with recessives the progenies segregated in the proportion of 7.2 resistants : 1 susceptible using strain C (Table 59). Had it inherited the dominant genes of both parents, $R_1R_2 \times R_1$, then a 3 : 1 ratio would be expected provided the two R1 genes remained independent from each other.

TABLE 59.

PROGENIES DERIVED FROM 1512d(4) AND 1514a(1) (882(5) x R_1 TYPE) CROSSED WITH RECESSIVE AND R_1R_2 TYPES.

Ref. No.	Parentage		Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1896	Bintje	× 1512*d*(4)	C	17	1	17·00 : 1	3 : 1	$r \times R_1R_1R_2$
1903*ab*	International Kidney	× 1512*d*(4)	C	72	8	9·00 : 1	3 : 1	
1908*abc*	King Edward VII	× 1512*d*(4)	C	91	16	5·69 : 1	3 : 1	
				180	25	7·20 : 1	3 : 1	
1913*a–e*	Up-to-Date	× 1514*a*(1)	C	145	217	0·67 : 1	1 : 1	$r \times R_1R_2$
1918*a*	882(5)	× do.	C	89	39	2·28 : 1	3 : 1	$R_1R_2 \times R_1R_2$
1918*b*	do.	× do.	F	66	26	2·54 : 1	3 : 1	
1981*ac*	1514*a*(1) Selfed		F	321	106	3·03 : 1	3 : 1	R_1R_2

The segregations indicate, however, that the chromosomes carrying the R_1 genes paired, and that the frequency of pairing was even greater than that normally occurring in an auto-tetraploid (5 : 1). Apparently affinity between the two chromosomes concerned was greater for each other than for the corresponding chromosomes lacking R_1 genes, since the frequency of pairing was about 50 per cent. Had their affinity been absolute, one R_1 gene would have been inherited by every plant, as in the case of a homozygous diploid, and all would have been resistant to strain C. Both auto-syndesis and allo-syndesis therefore occurred in 1512d(4), as in 1306a(15) and 1307a(23) already discussed.

In the double test (Table 60) the deficiency of C susceptibles is more or less equally divided between the C resistant-F susceptible segregates and the CF resistants, suggesting that half of the expected recessives and R_2 types had inherited gene R_1. If so, then the number of plants in the progeny possessing both R_1 genes will be correspondingly less. On the basis of 50 per cent. pairing of chromosomes carrying R_1 genes, the segregation would be such that in a theoretical progeny of 16, strain C would kill 2, strain F would kill 7, and 7 would survive. The observed ratios closely approximate these figures.

TABLE 60. /

TABLE 60.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Total	Genotypes (Significant Terms only)
1896	Bintje	× 1512*d*(4)	1	10	7	18	r × $R_1R_1R_2$
1903*ab*	International Kidney	× 1512*d*(4)	8	36	36	80	
1908*bc*	King Edward VII	× 1512*d*(4)	7	28	27	62	
		O	16	74	70	160	
		E	40	60	60	160	
		T	2	3	3	8	
			C	F			
1913*ab*	Up-to-Date	× 1514*a*(1)	83	22	27	132	r × R_1R_2
		O	66	33	33	132	
		E	2	1	1	4	
		T					
1918*a*	882(5)	× do.	39	27	62	128	$R_1R_2 \times R_1R_2$
		O	32	24	72	128	
		E	4	3	9	16	
		T					
			F	C			
1918*b*	do.	× do.	26	22	44	92	$R_1R_2 \times R_1R_2$
		O	23	17·25	51·75	92	
		E	4	3	9	16	
		T					

O = observed. E = expected. T = theoretical.

Another plant, 1514a(1), of similar origin (882(5) x R_1 type) proved to be resistant to C and F strains and to possess the genes R_1R_2 (Tables 59 and 60). When back-crossed to the female parent (882(5)) the theoretical segregation ratio is $1R_1R_1R_2R_2 : 2R_1R_1R_2 : 1R_1R_1 : 2R_1R_2R_2 : 4R_1R_2 : 2R_1 : 1R_2R_2 : 2R_2 : 1r$. Strain C kills the three R_2 types and the recessive (25 per cent.), strain F kills the three R_1 types (18.75 per cent.) and nine plants (56.25 per cent.) survive. If the sequence of strains is reversed the proportions remain the same, because the recessives succumb to the first strain applied.

The segregations obtained by crossing 882(5) (R_1R_2) with 1104 (R_3R_4) are shown in Table 61. The expected segregation is as follows :-

$1R_1R_2R_3R_4$ /

$1R_1R_2R_3R_4$	$1R_1R_2$	$1R_1$
$1R_1R_2R_3$	$1R_1R_3$	$1R_2$
$1R_1R_2R_4$	$1R_1R_4$	$1R_3$
$1R_1R_3R_4$	$1R_2R_3$	$1R_4$
$1R_2R_3R_4$	$1R_2R_4$	1r
	$1R_3R_4$	

Against strain B^2 only genes R_2 and R_3 are effective and a 3 : 1 ratio is obtained. Likewise against strain E only R_2 and R_4 are effective and a 3 : 1 ratio results.

TABLE 61.

PROGENIES DERIVED FROM 882(5) AND 1104.

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1518*d*	882(5) × 1104*a*(3)	B^2	116	37	3·14 : 1	3 : 1	$R_1R_2 \times R_3R_4$
1519*bc*	do. × do.	E	269	100	2·69 : 1	3 : 1	
1521*c*, 1522*a*	882(5) × 1104*c*(2)	B^2	356	136	2·62 : 1	3 : 1	
1921*de*, 1922*bc*	do. × do.	E	626	205	3·05 : 1	3 : 1	
1919*a*	882(5) × 1563*a*(18)	C	91	22	4·14 : 1	3 : 1	$R_1R_2 \times R_3$

In the double test (Table 62), where E is followed by C, all plants lacking genes R_2 and R_4 are killed (i.e. 25 per cent.) by strain E, and of the remainder those lacking genes R_1 and R_3 are killed by strain C (i.e. 18.75 per cent. of the original number). The survivors (56.25 per cent.) are resistant, not only to C and E but also to A, B^1, B^2 and D. In progeny 1919a, the pollen parent 1563a(18) was bred from Craigs Defiance x 1104a(3). The genes involved are R_3 and R_4, but since 1563a(18) is itself susceptible to strain E, it must /

must possess gene R_3 only.

TABLE 62.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by E	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1522*c*	882(5) × 1104*c*(2)	O	53	30	109	192	$R_1R_2 \times R_3R_4$
		E	48	36	108	192	
		T	4	3	9	16	
			C	F			
1919*a*	882(5) × 1563*a*(18)	O	22	41	50	113	$R_1R_2 \times R_3$
		E	28·25	42·375	42·375	113	
		T	2	3	3	8	

O = observed. E = expected. T = theoretical.

882(5) (R_1R_2) crossed with R_3 gives the segregation $1R_1R_2R_3 : 1R_1R_2 : 1R_1R_3 : 1R_2R_3 : 1R_1 : 1R_2 : 1R_3 : 1r$. The C strain kills the R_2 plants and the recessive (25 per cent.), and the F strain kills all the remainder which lack gene R_2 (37.5 per cent.). The survivors (37.5 per cent.) must possess at least gene R_2 together with either R_1 or R_3. Plants so constituted are resistant to at least nine ~~all seven~~ strains of the parasite.

The female parents, 1518d(2) and 1521c(6), referred to in Table 63 were bred from 882(5) x 1104 (R_1R_2 x R_3R_4), and were survivors of tests recorded in Table 61.

TABLE 63. /

TABLE 63.

PROGENIES DERIVED FROM SEEDLINGS OF (882(5) x 1104).

Ref. No	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1956*cd*	1518*d*(2) × 914*b*(52)	A	95	14	6·79 : 1	7 : 1	$R_2R_4 \times R_1$
1957*b*	do. × 1514*a*(1)	C	86	53	1·62 : 1	1 : 1	$R_2R_4 \times R_1R_2$
1957*a*	do. × do.	F	118	39	3·03 : 1	3 : 1	
1958*f*	1521*c*(6) × 23–22	B^2	63	20	3·15 : 1	3 : 1	$R_2R_3R_4 \times r$
1958*a–e*	do. × do.	C	265	369	0·72 : 1	1 : 1	

Seedling 1518d(2) proved to be susceptible to strain C and consequently it can possess neither R_1 nor R_3 genes. Since it is resistant to F, however, gene R_2 must be present. The presence also of gene R_4 is revealed by the A strain test of progeny 1956cd. The pollen parent of this progeny is an R_1 type, and the segregation ratio of 7 : 1 shows that three genes are in operation, two of which must be supplied by 1518d(2). The constitution of 1518d(2) is therefore R_2R_4, and when it is crossed with 1514a(1) (genotype R_1R_2 as shown in Table 59) the theoretical segregation is as follows :-

$1R_1R_2R_2R_4$	$1R_2R_2R_4$
$2R_1R_2R_4$	$2R_2R_4$
$1R_1R_2R_2$	$1R_2R_2$
$2R_1R_2$	$2R_2$
$1R_1R_4$	$1R_4$
$1R_1$	$1r$

In the double test (Table 64) strain F kills the segregates lacking gene R_2 (25 per cent.), and of the remainder strain C kills /

kills those lacking gene R_1 (37.5 per cent.). The survivors (37.5 per cent.) have at least R_1 and R_2 in their constitution. When strain C is used first it kills all genotypes lacking R_1 (50 per cent.). Of the remainder, strain F can kill only the R_1R_4 and R_1 types (12.5 per cent.), and the survivors are the same as before (37.5 per cent.).

Seedling 1521c(6) was found to be resistant to the F strain and must therefore possess gene R_2. In crosses with the recessive pollen parent 23-22 (Table 63) it gave progenies which segregated in approximately equal proportions in the C strain test, indicating the presence of either R_1 or R_3. The test with strain B^2 confirmed the gene as R_3, because the 3 : 1 segregation is possible only by the combined effect of R_2 and R_3. The presence of gene R_4 may also be assumed in view of the difference between the results of the double tests, C followed by E and C followed by F.

TABLE 64.

DOUBLE TESTS.

Ref. No.	Parentage		Killed by F	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1957*a*	1518*d*(2) × 1514*a*(1)	O	39	51	67	157	$R_2R_4 \times R_1R_2$
		E	39·25	58·875	58·875	157	
		T	4	6	6	16	
			C	F			
1957*b*	do. × do.	O	53	29	57	139	$R_2R_4 \times R_1R_2$
		E	69·5	17·375	52·125	139	
		T	8	2	6	16	
1958*cde*	1521*c*(6) × 23–22	O	229	66	81	376	$R_2R_3R_4 \times r$
		E	188	94	94	376	
		T	4	2	2	8	
			C	E			
1958*a*	do. × do.	O	77	19	41	137	$R_2R_3R_4 \times r$
		E	68·5	17·125	51·375	137	
		T	4	1	3	8	

O = observed. E = expected. T = theoretical.

Gene R_4 confers resistance to E but not to F, and hence the difference in the proportions observed. Thus the constitution of 1521c(6) is represented by $R_2R_3R_4$, and the theoretical segregation, on crossing with a recessive, is as follows : $1R_2R_3R_4$: $1R_2R_3$: $1R_2R_4$: $1R_3R_4$: 1R2 : $1R_3$: $1R_4$: 1r. In the double test, strain C kills all plants lacking gene R_3 (50 per cent.), strain F kills the R_3 and R_3R_4 types (25 per cent.), and the $R_2R_3R_4$ and R_2R_3 types survive (25 per cent.). When strain E is employed instead of strain F only the R_3 types are killed (12.5 per cent.), and the $R_2R_3R_4$, R_2R_3 and R_3R_4 types survive (37.5 per cent.).

Progenies tested with Mixtures of Strains.

In Table 65 are shown the segregations obtained in progenies after inoculation with certain mixtures of strains.

TABLE 65.

PROGENIES DERIVED FROM 1512c(11), 1512c(16) AND 1512d(11) (882(5) x R_1 TYPE) CROSSED WITH RECESSIVE, R_1, R_3 AND R_3R_4 TYPES.

REF. NO.	PARENTAGE	STRAINS	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
2071a-d	1512c(11) x 11-79	CF	58	178	0.98:3	1:3	R_1R_2 x r
2073ab	1512c(16) x Aquila	CF	56	199	0.84:3	1:3	R_2 x R_1
2161ab	do. x 1306a(2)	CF	79	194	1.22:3	1:3	R_2 x R_3R_4

2163a /

TABLE 65 (contd.).

REF. NO.	PARENTAGE	STRAINS	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
2163a	1512d(11) x 11-79	CF	25	106	0.71:3	1:3	R_1R_2 x r
2078a	do. x Aquila	CF	41	67	3.06:5	3:5	R_1R_2 x R_1
2165ab	do. x 1573(10)	CGF	45	184	0.73:3	1:3	R_1R_2 x R_3
2164de	do. x 1306a(2)	CF	93	183	2.54:5	3:5	R_1R_2 x R_3R_4
2164bc	do. x do.	CGF	53	102	5.71:11	5:11	do.

The female parents, 1512c (11), 1512c(16) and 1512d(11) were bred from 882(5)(R_1R_2) x 834c(29)(R_1) and their reactions to the various strains show that 1512c(11) and 1512d(11) posess genes R_1 and R_2 while 1512c(16) has gene R_2 only. Of the varieties employed as male parents, only one, 1573(10) has not featured in previous Tables. 1573(10) was bred from recessive x 1306a(2)(R_3R_4) and was found to have inherited gene R3.

Table 65 shows that in progenies derived from R_1R_2 x r or R_2 x R_1 and tested with a mixture of strains C and F, only the R_1R_2 segregates survive. Such progenies thus give a ratio of approximately 1 resistant : 3 susceptibles. A similar ratio is obtained in progenies derived from R_2 x R_3R_4 because gene R_4 is ineffective against both C and F and gene R_3 reacts towards them in the same manner as gene R_1. For the same reason progenies bred from R_1R_2 x R_1 give the same segregation ratio as those bred from R_1R_2 x R_3R_4 when strains C and F are used. In these cases the ratio /

ratio is 3 resistants : 5 susceptibles, the resistant segregates being the plants with at least R_1R_2 in their constitution in the first case and at least R_1R_2 or R_2R_3 in the second.

When a mixture of strains C, G and F is used for testing a progeny derived from R_1R_2 x R_3 a ratio of 1 resistant : 3 susceptibles is obtained in accordance with the genotypic segregation $1R_1R_2R_3$ / $1R_1R_2$: $1R_1R_3$: $1R_2R_3$: $1R_1$: $1R_2$: $1R_3$: $1r$. Here the only plants resistant to all three strains are the $R_1R_2R_3$ and the R_2R_3 types. The same mixture of strains applied to seedlings bred from R_1R_2 x R_3R_4 gives a ratio of 5 resistants : 11 susceptibles, the resistants in this case being the $R_1R_2R_3R_4$, $R_1R_2R_3$, $R_1R_2R_4$, $R_2R_3R_4$ and R_2R_3 types.

TABLE 66.

PROGENIES DERIVED FROM 1564a(15), 1584c(10) AND 1584c(16) (RECESSIVE X 1104c(2)) CROSSED WITH RECESSIVE, R_2 AND R_2R_3 TYPES.

REF. NO.	PARENTAGE	STRAINS	NUMBER OF SEEDLINGS R	NUMBER OF SEEDLINGS r	RATIO OBSERVED	RATIO THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY
2083a-e	1564a(15) x 11-79	C	281	335	0.84:1	1:1	R_3R_4 x r
2082a-c	do. x 1508b(3)	CF	17	60	0.85:3	1:3	R_3R_4 x R_2
2168a-d	1584c(10) x 11-79	B^2	174	152	1.14:1	1:1	R_3R_4 x r
2170a-f	do. x 1682c(1)	CF	113	195	2.90:5	3:5	R_3R_4 x R_2R_3
2171ab	1584c(16) x 11-79	B^2	139	147	0.95:1	1:1	R_3R_4 x r
2173a-d	do. x 1682c(1)	CF	35	52	3.37:5	3:5	R_3R_4 x R_2R_3

In Table 66 the female parents involved, viz. 1564a(15), 1584c(10) and 1584c(16) were bred from recessive x 1104c(2)(R_3R_4) and all are alike in having the genetic constitution R_3R_4. The only male parent not previously discussed is 1682c(1) which, on the basis of its reactions to the various strains, is an R_2R_3 type.

Progenies derived from R_3R_4 x r segregate resistants and susceptibles in equal proportions when inoculated with either strain C or strain B^2 because the R_4 gene is ineffective against both while the R_3 gene confers resistance to both. Inoculation of seedlings bred from R_3R_4 x R_2 with a mixture of strains C and F gives a 1 : 3 ratio since only two, viz. $R_2R_3R_4$ and R_2R_3, of the eight possible genotypes resist both strains. When the same two strains are applied to progenies derived from R_3R_4 x R_2R_3 the resulting ratio is 3 resistants : 5 susceptibles since only those segregates possessing R_2 and R_3 genes can withstand the attack of strains C and F.

Female parent 1647b(1) (Table 67) was bred from 655(43) (R_1 type) x 1318(3) (R_2 type) and was found to have the constitution R_1R_2.

TABLE 67.

PROGENIES DERIVED FROM 1647b(1) (R_1 TYPE x 1318(3)) CROSSED WITH RECESSIVE, R_1, R_2R_3 and R_3R_4 TYPES.

REF. NO.	PARENTAGE		STRAINS	NUMBER OF SEEDLINGS R	r	RATIO OBSERVED	THEORETICAL	GENOTYPES (SIGNIFICANT TERMS ONLY)
2093a-d	1647b(1)	x 11-79	CF	94	318	0.89:3	1:3	R_1R_2 x r
2091a-d	do.	x Aquila	CF	71	128	2.77:5	3:5	" x R_1
2176	do.	x 1682c(1)	CGF	23	51	2.25:5	3:5	" x R_2R_3
2175c	do.	x 1306a(2)	CF	25	53	2.36:5	3:5	" x R_3R_4
2175abd	do.	x do.	CGF	113	250	4.97:11	5:11	" x "

With one exception, the genotypes employed as parents in this Table as well as the inoculum used, are identical with examples presented in Table 65 and consequently need not be further discussed. These are R_1R_2 x r, R_1R_2 x R_1 and R_1R_2 x R_3R_4. The exception is R_1R_2 x R_2R_3, the reference number of which is 2176. The seedlings of this cross would be expected to segregate as follows:-

$1R_1R_2R_2R_3$	$1R_1R_2R_2$	$1R_1R_3$
$2R_1R_2R_3$	$2R_1R_2$	$1R_3$
$1R_2R_2R_3$	$1R_2R_2$	$1R_1$
$2R_2R_3$	$2R_2$	1r

When inoculated with a mixture of strains C, G and F, only those plants posessing genes R_2 and R_3 (grouped together in the first column) would survive. The ratio would accordingly be 6 resistants : 10 susceptibles, i.e. 3 : 5.

TABLE 68.

SEGREGATIONS OBTAINED IN FAMILY 2070ab(R_1R_2 x R_3R_4) BY INOCULATING DETACHED LEAVES.

STRAIN		NUMBER OF SEEDLINGS R	r	TOTAL
A (Group I)	O	66	8	74
	E	69.375	4.625	74
	T	15	1	16

H /

TABLE 68 (contd.)

STRAIN		NUMBER OF SEEDLINGS R	r	TOTAL
H (Group II)	O	63	11	74
	E	64.75	9.25	74
	T	7	1	8
D (Group II)	O	60	14	74
	E	64.75	9.25	74
	T	7	1	8
G (Group III)	O	53	21	74
	E	55.5	18.5	74
	T	3	1	4
B^2 (Group III)	O	52	22	74
	E	55.5	18.5	74
	T	3	1	4
C (Group III)	O	54	20	74
	E	55.5	18.5	74
	T	3	1	4
F (Group IV)	O	30	44	74
	E	37	37	74
	T	1	1	2

O = observed. E = expected. T = theoretical.

Table 68 shows the results obtained from progeny 2070ab when tested, by means of the detached leaf method, with seven different strains of blight. This progeny was bred from 1512c (11)(R_1R_2) x 1306a(2)(R_3R4) and would therefore be expected to contain all the possible combinations of the four different R genes. The main feature of the Table is that Group I (strain A) gives a ratio of 15 resistants : 1 susceptible; Group II (strains H and D) gives 7 resistants : 1 susceptible; Group /

Group III (strains G, B^2 and C) gives 3 resistants : 1 susceptible; and Group IV (strain F) gives 1 resistant : 1 susceptible.

By means of these leaf tests it has been possible to determine the genetic constitution of approximately 50% of the seedlings in family 2070ab. The remainder cannot be differentiated with accuracy until further strains are available or progeny tests have been made.

Classification of Fungal Strains.

It has been shown that resistance to the various strains of blight is manifested in the presence of major genes derived from S. demissum and that four such genes are distinguishable in this material, viz. R_1, R_2, R_3 and R_4. Each gene, when present in the plant, induces a hypersensitive response to infection with the common strain and with a particular group of specialised strains of the parasite. All four genes are inherited independently in simple Mendelian fashion.

Since dominance of these R genes is complete, it follows that the maximum number of different phenotypic reactions which can be distinguished by direct tests with the different strains of the parasite is sixteen. This series represents the complete range of hosts differential for the material in question and is capable of distinguishing sixteen different strains of the parasite.

The reactions of the sixteen host types to the available strains /

strains are shown in Table 69.

TABLE 69.

INTERRELATIONSHIPS OF GENES AND STRAINS.

GENOTYPES	STRAINS OF PHYTOPHTHORA INFESTANS														
	A	B^1	H		D	G	E	B^2		C	I			F	
	0	(1)	(2)	(3)	(4)	(1, 2)	(1, 3)	(1, 4)	(2, 3)	(2, 4)	(3, 4)	(1, 2,3)	(1, 2,4)	(1, 3,4)	(2, 3,4)	(1,2, 3,4)
r	+	+	+	⊹	+	+	+	+	⊹	+	+	⊹	⊹	+	⊹	⊹
R_1	−	+	−	·····	−	+	+	+	·····	−	−	⊹	⊹	+	·····	⊹
R_2	−	−	+	·····	−	+	−	−	⊹	+	−	⊹	⊹	−	⊹	⊹
R_3	−	−	−	⊹	−	−	+	−	⊹	−	+	⊹	·····	+	⊹	⊹
R_4	−	−	−	·····	+	−	−	+	·····	+	+	·····	⊹	+	⊹	⊹
R_1R_2	−	−	−	·····	−	+	−	−	·····	−	−	⊹	⊹	−	·····	⊹
R_1R_3	−	−	−	·····	−	−	+	−	·····	−	−	⊹	·····	+	·····	⊹
R_1R_4	−	−	−	·····	−	−	−	+	·····	−	−	·····	⊹	+	·····	⊹
R_2R_3	−	−	−	·····	−	−	−	−	⊹	−	−	⊹	·····	−	⊹	⊹
R_2R_4	−	−	−	·····	−	−	−	−	·····	+	−	·····	⊹	−	⊹	⊹
R_3R_4	−	−	−	·····	−	−	−	−	·····	−	+	·····	·····	+	⊹	⊹
$R_1R_2R_3$	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	⊹	·····	·····	·····	⊹
$R_1R_2R_4$	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	⊹	·····	·····	⊹
$R_1R_3R_4$	−	−	−	·····	−	−	−	−	·····	−	−	·····	·····	+	·····	⊹
$R_2R_3R_4$	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	·····	⊹	⊹
$R_1R_2R_3R_4$	−	−	−	·····	−	−	−	−	·····	−	−	·····	·····	−	·····	⊹

− RESISTANT
+ SUSCEPTIBLE } OBSERVED
····· RESISTANT
⊹ SUSCEPTIBLE } THEORETICAL

The strains are arranged, not in alphabetical order as collected, but in accordance with their individual effects on the differential series. From this Table, it appears that for each of the sixteen host genotypes a specially adapted strain of Phytophthora is theoretically possible. These genotypes will be referred to as the "natural" hosts of the strains specially adapted to them. Ten of the strains have now been isolated and classified in accordance with the reactions which they induce in the differential host series. The reactions to be expected from inoculation with the six hypothetical strains are included in the Table in order to provide a complete picture of the host-parasite relationships possible in the present experiments. The specialised strains and the genotypes to which they are best adapted may be traced from the diagonal of + signs, e.g. genotype R_1 appears as the natural host of strain B^1, genotype R_1R_3 as the natural host of strain B^2 and genotype $R_1R_3R_4$ as the natural host of strain F.

It will be seen that strain B^1 can attack only the recessive and R_1 types while the host range of strain F is much wider. The natural host of strain F emerges as genotype $R_1R_3R_4$ but this strain also parasitises all genotypes lacking R_2 in their constitution, viz. R_1, R_3, R_4, R_1R_3, R_1R_4 and R_3R_4 together with the recessive. The host ranges of all the strains may be found in the same way.

This Table thus shows at a glance the complete range of relationships between host genotypes and strains of the parasite /

parasite obtainable in the present experiments. It provides a genetical basis for the classification of strains and a key for the calculation of segregation ratios resulting from the mating of any pair of genotypes when infected with any strain or group of strains of P. infestans.

By crossing genotype R_1R_2 with genotype R_3R_4 it is theoretically possible to obtain all the genotypes enumerated. Many such progenies have been raised in recent years but, since the complete series of specialised strains has not been found, it is impossible to confirm the presence of several of these genotypes. On the evidence of those which have been identified and the proportions in which they occurred, there is no reason to doubt that the complete series of genotypes segregates in accordance with theoretical expectation.

In view of the lack of information regarding the pathogenicity of strains of Phytophthora infestans and the hereditary constitution of blight resistant material in countries overseas, arrangements were made in 1951 with Dr. Mastenbroek in Holland and Professor Reddick and Professor Peterson in America for the exchange of differential host varieties together with data relating to the respective collections of Phytophthora strains. The results of the tests carried out on these differential host varieties have been co-ordinated with the information supplied (see Table 70). Comparison of the differential host series show that no new genes are present in either the Dutch or the American varieties and that both these /

these series contain genes R_1, R_2 and R_4 but not R_3.

TABLE 70.

COMPARISON OF DIFFERENTIAL HOSTS OF REDDICK AND PETERSON, MASTENBROEK, AND BLACK.

GENO-TYPE	DIFFERENTIAL HOSTS OF			STRAINS OF PHYTOPHTHORA INFESTANS																
	REDDICK & PETERSON			A	D	C	B			BD			BC		BCD					
		MASTENBROEK		N1	N2	N5	N4			N7			N6		N8		N9			
			BLACK	A	B^1	H	D	G	E	B^2	C	I	F							
r	S.tub.	S.tub.	S.tub.	+	+	+	+	+	+	+	+	+	+	+	+					
R_1	Essex	43154-5	1085(6)	−	+	−	−	+	+	+	−	−	+	+	−					
R_2	ZLY/13	44158-4	1512c(16)	−	−	+	−	+	−	−	+	−	+	−	+					
R_3			1253a(12)	−	−	−	−	−	+	−	−	+	+							
R_4	AAB/2	4431-5	1506b	−	−	−	+	−	−	+	+	+	+	+	+					
R_1R_2	GQT/1	4651-2	1647b(1)	−	−	−	−	+	−	−	−	−	+	−	−					
R_1R_3			1661b(7)	−	−	−	−	−	+	−	−	−	+							
R_1R_4		46174-30	1506b(9)	−	−	−	−	−	−	+	−	−	+	+	−					
R_2R_3			1682c(1)	−	−	−	−	−	−	−	−	−	−							
R_2R_4	CDF/9	4414-2	2070(31)	−	−	−	−	−	−	−	+	−	+	−	+					
R_3R_4			1488b(1)	−	−	−	−	−	−	−	−	+	+							

The data relating to collections of strains in Holland and America fit into the general scheme of relationships between genes and strains described in Table 69. It is apparent that one of the seven strains of Reddick & Peterson, and two of the eight strains

of /

of Mastenbroek are unknown in Scotland. The three collections of strains thus contain amongst them twelve of the sixteen strains referred to in Table 69.

The comparisons of the above material made by Mastenbroek in Holland have recently been published (Mastenbroek 1952) and are in agreement with the present findings. Included in Mastenbroek's data is a plant which reacts to the various strains in a manner identical with the R_3 genotype. This plant was discovered too late to be included in the differential host series kindly supplied by Mastenbroek in 1951.

Prolificacy of Strains.

The nine specialised strains included in Table 69 may be classified into three main groups according to the number of different genes possessed by the natural host of each strain. They are :-

Group 1. Parasitises plants with not more than 1 "R" gene.
" 2. " " " " " " 2 different "R" genes.
" 3. " " " " " " 3 different "R" genes.

These three groups appear to represent three progressive stages in evolution towards a wider host range and ultimately to a possible universal strain capable of attacking all genotypes. In the course of these changes, the pathogenicity of the different specialised strains towards commercial varieties /

varieties of S. tuberosum would be expected to differ from each other and from the common strain from which they evolved. If such differences do prevail they should be reflected in the numbers of sporangia produced and consequently in the survival value of the different strains in competition with each other.

In order to test this assumption, spore suspensions of strains C and F were made using equal quantities of water. Samples of the suspensions examined under the microscope showed that the sporangia of strain F were 33.3% more numerous than those of strain C. The two suspensions were then thoroughly mixed and sprayed on detached leaves of S. tuberosum var. Craigs Royal. The culture so obtained was repeatedly passed through Craigs Royal at seven day intervals using the sporangia produced at each passage for the next inoculation. In order to obtain a record of the persistence of each strain, two filter varieties, viz. 1512c(16)(R_2) and 1488b(1)(R_3R_4) were also inoculated at each stage in the experiment. At the end of the first passage both filter varieties produced a heavy crop of sporangia, that on 1512c(16) consisting entirely of strain C and that on 1488b(1) consisting entirely of strain F. The density of sporulation occurring on these filter varieties provides a measure of the composition of the inoculum used. It will be seen from Table 71 that the crops of sporangia produced by Craigs Royal and 1512c(16) were abundant throughout, while the crop on 1488b(1) became less with each successive passage through Craigs Royal and was entirely absent in the fourth test. This shows that the inoculum obtained from Craigs Royal at the

end /

end of the third passage consisted of strain C only, and that strain F had gradually disappeared in the course of three passages through Craigs Royal. The survival value of strain F is, therefore, very low in competition with strain C when grown on S. tuberosum.

TABLE 71.

RELATIVE SURVIVAL VALUE OF STRAINS C AND F CULTURED ON CRAIGS ROYAL.

		SPORULATION 7 DAYS AFTER INOCULATION.			
Variety	Genotype	1st passage	2nd passage	3rd passage	4th passage
Craigs Royal	r	Abundant	Abundant	Abundant	Abundant
1512c(16)	R_2	Abundant	Abundant	Abundant	Abundant
1488b(1)	R_3R_4	Abundant	Sparse	Very sparse	None

In a similar manner the survival values of six strains (A, B^2, C, D, E and F) were tested, (Table 72). Suspensions of each, containing approximately equal numbers of sporangia were mixed and passed through Craigs Royal ten times. At each stage, leaves of the differential host varieties were also inoculated in order to ascertain the relative persistence of the different strains in competition on Craigs Royal. It was found that strain F had ~~almost~~ disappeared after the third passage as shown /

shown by 1488b(1), strain E was lost after the sixth as revealed by 1253a(12) and strain B^2, although it survived the ten passages, was greatly reduced in density of sporulation as indicated by 835a(4) and 1506b(9). Strain C continued to sporulate abundantly throughout.

TABLE 72.

RELATIVE SURVIVAL VALUE OF STRAINS A, B^2, C, D, E AND F CULTURED ON CRAIGS ROYAL.

Variety	Genotype	SPORULATION AT EACH PASSAGE 7 DAYS AFTER INOCULATION. 1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th
Craigs Royal	r	1111	1111	1111	1111	1111	1111	1111	1111	1111	1111
835a(4)	R_1	1111	111	111	111	111	11	11	11	11	11
1512c(16)	R_2	1111	1111	1111	1111	1111	1111	1111	1111	1111	1111
1253a(12)	R_3	1111	111	111	11	11	1	0	0	0	0
1506b	R_4	1111	1111	1111	1111	1111	1111	1111	1111	1111	1111
1506b(9)	R_1R_4	1111	1111	1111	1111	111	111	11	11	11	11
1488b(1)	R_3R_4	1111	11	1	0	0	0	0	0	0	0

1111 = Abundant
111 = Medium
11 = Sparse
1 = Very Sparse
0 = None

Presumably strains A and D also survived the ten passages without difficulty but it was impossible to confirm their presence because the natural hosts of A and D are also susceptible to C. Strain C was /

was found to be more prolific than B^2 and much more prolific than E on S. tuberosum, although all three fall into the group which parasitises plants carrying two different major genes. Nevertheless, in both experiments the first strain to disappear was F which has a wider host range than any of the others employed in the comparison, being the only strain capable of attacking a plant carrying three different R genes. The results suggest that the wider the host range of a strain the less prolific it is on recessive varieties and the lower is its survival value in competition with less specialised forms. Accordingly, if all these strains were released in a field crop of S. tuberosum the specialised strains would gradually disappear, those with wider host ranges going first, until eventually only the common strain would remain. How long this process of elimination would require for completion is unknown, but possibly more than one season. In any event, the specialised strains must be regarded as less virulent than the common strain in relation to S. tuberosum.

Since the persistence of a strain depends largely upon its reproductive capacity in the environment of the plant it parasitises, it is unlikely that a specialised strain would be equally prolific on the different genotypes that are susceptible to it. In order to examine this point, strain C was employed for the inoculation of three varieties of S. tuberosum, and one representative /

representative each of genotypes R_1, R_2, R_3, R_4 and R_3R_4. Detached leaflets of similar surface area were uniformly inoculated, and a comparison was made of the crops of sporangia produced on the sixth day and again on the eighth day after inoculation, (Table 73). The estimations were made by counting, with the aid of a microscope, the number of sporangia in samples of the suspensions obtained from the leaflets, using standard quantities of water.

TABLE 73.

RELATIVE PROLIFICACY OF STRAIN C CULTURED ON DIFFERENT HOST GENOTYPES.

Host	Genotype	No. of Sporangia * at 6 days	No. of Sporangia * at 8 days
Arran Victory	r	43	329
Craigs Royal	r	23	173
Home Guard	r	28	167
835a(4)	R_1	0	0
1215c(16)	R_2	53	433
1253a(12)	R_3	0	0
1786a	R_4	77	452
1488b(1)	R_3R_4	0	0

* Total of 9 samples in each case.

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The figures show that spore production varies greatly between different host genotypes. No sporangia were found on genotypes R_1, R_3 and R_3R_4 since these plants are hypersensitive to strain C. The largest numbers of sporangia occurred on the R_4 and R_2 genotypes both of which are susceptible to strain C. A significant feature of the results was the relatively low counts of sporangia obtained from the S. tuberosum varieties, suggesting that strain C is better adapted to R_2 and R_4 forms than to the recessives. At the same time, the recessives showed differences which indicate that Arran Victory is more susceptible than Home Guard and Craigs Royal — differences which have been borne out in field observations. These differences between varieties of S. tuberosum are attributed to differences in minor gene complexes.

On the above evidence, the reproductive capacity of a strain is dependent primarily upon the genetic constitution of the host. Strains are, on the whole, most prolific on the plant genotypes to which they are specially adapted. Although all the strains employed are capable of attacking S. tuberosum, it appears that those with the widest host range are least prolific on S. tuberosum. Lehmann (1938) and Schaper (1949) observed a slower growth of specialised races on tubers and leaves of S. tuberosum varieties.

In this light, the common strain of blight is so-called simply because it is the one best adapted to the common commercial varieties bred from S. tuberosum and is consequently more prolific than any other strain in such an environment.

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But the common strain is not strictly uniform, because minor differences in the infective power of isolates have been observed both in foliage and in tuber tests. The common strain may, therefore, be more accurately described as a population within which variation exists but which is maintained at an equilibrium by its environment, principally by its host. The variants within it, if they persist, must be equally prolific, since the less prolific forms would gradually disappear. Mutations probably occur frequently, but the survival of mutant forms must be dependent upon their reproductive capacity on the host plants with which they came in contact. If hyphal growth should be slower or sporulation less prolific than that of the parent population, they would not survive. The discovery of new strains is thus dependent upon the meeting of variants or mutants with the particular genotypes to which they are adapted.

Source of Fungal Strains.

Although the exact mode of origin of specialised strains remain problematical, the source of some of them is reasonably clear. According to Reddick and Mills (1938, 1939), new strains may be produced by repeated passages of a culture through a variety that is resistant to it. A special technique is required to enable the fungus to sporulate until it becomes "adapted" to the new host. Thus, the virulence of a strain may be so increased that a plant which was previously resistant, becomes /

becomes normally susceptible. Mills (1940) was able to change a potato strain to a tomato strain by seven passages through tomatoes. Similar examples of adaptation were reported by de Bruyn (1951). Not only could strains be increased in virulence by such treatment; they could also be decreased. In interpreting her results, de Bruyn observed that "The gradual and reversible character of the changes makes it rather difficult to ascribe the phenomenon to nucleus alteration. Still, such nuclear change may be the correct explanation." Whatever the explanation, such changes do occur. The agency determining the direction of the change, however, is difficult to identify unless the genetical constitution of the host plants is known.

During the course of the present experiments, several instances of alteration in pathogenicity have been recorded, but most of them occurred naturally without any intentional manipulation to encourage change. In this manner, strain A changed to D, strain B^1 changed to B^2, strain E changed to F and strain I changed to F. These changes took place in the course of experiments with genetically mixed material which included suitable host genotypes for the altered strains in each case. A planned attempt to change strain D to strain C by repeated culture on detached leaves of a plant with the genetic constitution R_2 was successful, requiring only four passages to attain normal sporulation. It seems probable that all the above changes could be effected by the techniques employed /

employed by Reddick and Mills and by de Bruyn.

In other cases, repeated attempts to alter pathogenicity ended in failure. Although B^1 changed to B^2 without manipulation, the former could not be changed to D in a planned experiment. Similarly, no success attended attempts to synthesise the missing natural strain of genotype R_3 either from strain B^1 or strain D. These attempts were made by inoculating detached leaves of the appropriate plants grown under glasshouse conditions. The slowly dying leaves tended to become waterlogged and sporangia for further inoculation were obtained only after an extended incubation period of approximately four days beyond the normal for susceptible varieties. The number of passages which were successfully completed varied from one to six in the different experiments before the cultures finally died out. Comparable failures have been reported by Müller (1935, 1936) and Bonde, Stevenson and Clark (1940).

These various successes and failures suggest that alterations in the host range of strains may take place only in certain directions. On the basis of the data contained in Table 69 it may be assumed that the common strain gave rise to B^1, H and D but it is unlikely that B^1, H and D can give rise to each other or to the natural strain of genotype R_3. B^1, presumably, gave rise to B^2 and D to C but none of the members of the group which includes B^2 and C are recorded as having been the source of another member of that group. Similarly, E and I gave rise to F.

On such evidence, it appears that specialisation proceeds /

proceeds along particular lines only and that these lines are determined by the genetic relationships of the hosts. Since, for example, genotype R_1 is directly related to genotypes R_1R_2, R_1R_3 and R_1R_4, strain B^1 could be the progenitor of strains G, E and B^2. Similarly, since genotype R_4 is directly related to R_1R_4, R_2R_4 and R_3R_4, strain D could give rise to strains B^2, C and I. If this principle be applied throughout the series, a diagram of progressive specialisation may be drawn as shown in Fig. 5. For simplicity in following the direction of specialisation indicated by this scheme, the designations of the strains have been changed to correspond with the genetic constitution of the natural host plants in each case. Thus, strain D becomes strain (4) because R_4 is the constitution of its natural host and strain C becomes strain (2,4) because R_2R_4 is the constitution of its natural host.

From the lines in the diagram, it appears that the common strain, designated O, may give rise to strains (1), (2), (3) and (4) and that strain (1) in turn may give rise to strains (1,2), (1,3) and (1,4) but not to (2,3), (2,4) or (3,4). Likewise, strain (1,2) may give rise to strain (1,2,3) and (1,2,4) but not to (1,3,4) or (2,3,4). The direction of development of other strains may be followed in the same manner. It thus appears that strain (1) after passing through two phases of specialisation can give rise to strains (1,2,3), (1,2,4) and (1,3,4) but not to strain (2,3,4); similarly, strain (2) may give rise to strains (1,2,3), /

(1,2,3), (1,2,4) and (2,3,4) but not to (1,3,4) and so on. It will be seen from the diagram that specialisation need progress only one further stage in order to produce a strain capable of attacking all the known genotypes. Whether this can occur is unknown. No evidence is available to indicate that specialisation has reached its limit at the third stage apart from the continued freedom from blight of the original S. demissum.

Apart from these theoretical possibilities, Fig. 5 illustrates the host range of each of the strains in question. The natural host genotype of any particular strain is susceptible to all strains connected by lines to the right of it and is resistant to the remainder. As an example, genotype R_1R_2 is susceptible to strains (1,2), (1,2,3), (1,2,4) and (1,2,3,4) and is resistant to all other strains included in the diagram.

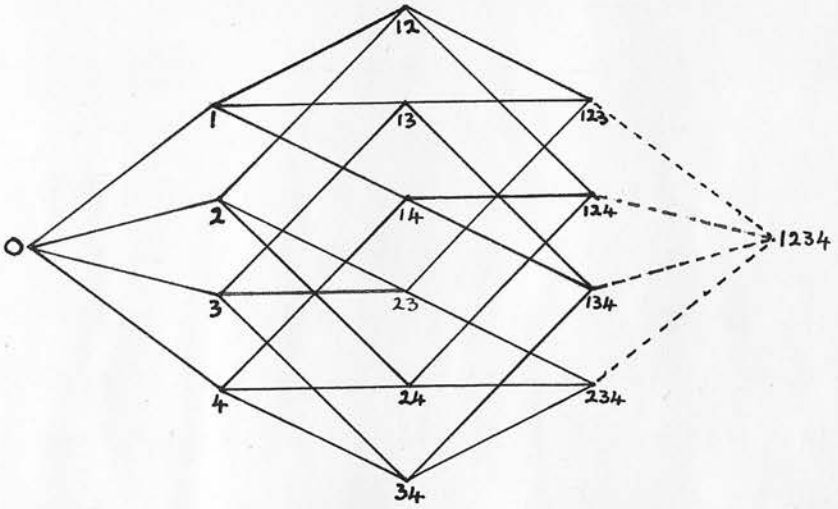

Fig. 5.

DISCUSSION.

Fully twenty years ago Müller (1930) showed that the inheritance of resistance to Phytophthora infestans in the potato is complex. The segregations he observed could not be compared strictly with standard Mendelian ratios, and the findings were explained by postulating four allelomorphic genes of different numerical value. Resistance was attained in a plant only when the sum of these values in its genotype reached a certain numerical level. Later, an investigation was made by Lehmann (1941) in an attempt to assess the potentialities of nine varieties of the species S. demissum as a genetic source of resistance. In all crosses between resistant and susceptible forms, the whole F_1 generation was found to be resistant. Further, the segregations in F_2 and in back-cross generations showed that the differences in resistance were conditioned by Mendelian genes. The mode of inheritance was found to be the same for resistance to the two different strains of Phytophthora employed, and reciprocal crosses gave identical results. Apparently the lack of a suitable series of Phytophthora biotypes or strains prevented the differentiation of genes in these experiments.

The main feature of the present experiments is the identification in the hereditary constitution of S. demissum (CPC 2127) of four different major genes each conferring different /

different and distinct reactions to infection with strains of Phytophthora infestans. The existence of three of these genes had been established for some time, but it was only with the discovery of a fourth gene that several early results, apparently anomalous, could be fully explained and the range of data fitted to a relatively simple Mendelian scheme. No evidence of the existence of any further major genes in CPC 2127 has come to light. In the elucidation of the inheritance of resistance to blight, the triple hybrid material derived from (S. Rybinii x S. demissum) X S. tuberosum provided not only the cytological balance for genetical purposes but also pollen fertility which is so frequently absent in commercial varieties. In an examination of this material Thomas (1945) found that chromosome differentiation between the species involved was not sufficient to affect pairing to any extent.

The identity of the individual genes could not be fully established in the early generations of the experiments because of the lack of sufficient strains of the parasite and the obscurity of the segregations caused by the presence of more than one gene. In later generations, when the genes had become separated by means of back-crossing to recessives, it became possible to study them individually and to establish that the mode of inheritance was similar in each case and in conformity with Mendelian principles. However, three important deviations from standard disomic ratios were observed. The first occurred in early generations derived from S. demissum (2n = 72) and S. tuberosum (2n = 48) when chromosome /

chromosome numbers were irregular and unpaired chromosomes were frequent. The expected Mendelian ratios were not obtained in this case due to the frequency of inclusion of unpaired chromosomes carrying resistance genes. Similar irregularities in chromosome behaviour with consequent breeding results have been recorded by Salaman (1928), Becker (1939), Schnell (1948), Howard and Swaminathan (1952) and others.

The second type of deviation occurring in apparently normal tetraploid material was characterised by a consistent excess of recessive segregates in certain parental combinations, particularly in back-crosses to varieties of S. tuberosum. This appeared to be due to differences in the frequency of fusion of different kinds of gametes and was ascribed to the action of minor incompatibility factors introduced in the original hybridisation. Though the extent of the deviations from normal ratios were variable, they suggest by their uni-directional variance that influences other than pure chance were in operation. In order to compare the average deviations of several groups of progenies, the totals have been brought together in Table 74 and tested for goodness of fit. It will be seen that some of the segregations show a reasonably good approximation to simple Mendelian ratios while in other cases the probability is extremely small.

TABLE 74. /

TABLE 74.

TOTALS OF GROUPS IN TABLES 20, 26, 30, 3, 4, 5, 6.

Table	Expected R	Expected r	Observed R	Observed r	No. of Seedlings R	No. of Seedlings r	Total	χ^2	Deviation D.F.	Deviation P
20	1	1	0.86	1	336	392	728	4.30	1	0.05-0.02
	1	1	0.89	1	1399	1569	2968	9.74	1	Small
	3	1	2.03	1	1159	572	1731	59.74	1	Very small
26	1	1	1.05	1	164	156	320	0.20	1	0.70-0.50
	1	1	0.92	1	707	772	1479	2.86	1	0.10-0.05
	1	1	0.76	1	126	165	291	5.23	1	0.05-0.02
	3	1	2.72	1	403	148	551	1.02	1	0.50-0.30
	3	1	2.87	1	456	159	615	0.24	1	0.70-0.50
	15	1	10.15	1	274	27	301	3.81	1	0.10-0.05
30	1	1	0.61	1	189	311	500	29.77	1	Very small
	3	1	2.83	1	147	52	199	0.14	1	0.80-0.70
	15	1	10.13	1	324	32	356	4.56	1	0.05-0.02
3	1	1	0.72	1	902	1245	2147	54.80	1	Very small
	3	1	1.77	1	237	134	371	24.46	1	Very small
4	1	1	0.83	1	925	1119	2044	18.41	1	Very small
5	1	1	0.93	1	1246	1337	2583	3.21	1	0.10-0.05
6	3	1	2.79	1	760	272	1032	1.01	1	0.50-0.30

The progenies derived from the triple hybrids (Tables 20, 26,30) are further condensed in Table 75, and those from the multiple hybrid W.800(2) (Tables 3, 4, 5, 6) in Table 76.

TABLE 75.

TOTALS DERIVED FROM TRIPLE HYBRIDS (TABLES 20, 26, 30).

Expected R	Expected r	Observed R	Observed r	No. of Seedlings R	No. of Seedlings r	Total	χ^2	Deviation D.F.	Deviation P.
1	1	0·87	1	2921	3365	6286	31·36	1	Very small
3	1	2·32	1	2165	931	3096	42·46	1	Very Small
15	1	10·14	1	598	59	657	8·36	1	Small

TABLE 76.

TOTALS DERIVED FROM MULTIPLE HYBRID (TABLES 3, 4, 5, 6).

Expected R r	Observed R r	No. of Seedlings R	r	Total	χ^2	Deviation D.F.	P.
1 : 1	0·83 : 1	3073	3701	6774	58·22	1	Very small
3 : 1	2·46 : 1	997	406	1403	11·60	1	Small

Although the triple hybrids inherited their resistance from S. demissum alone, while W.800(2) had two sources, S. demissum and S. edinense, these two groups of seedlings show a close similarity in their corresponding segregations.

Table 77 contains the combined data of Tables 75 and 76. Analysis of these grand totals shows that the segregations as a whole do not agree with standard theoretical ratios. Unbalanced segregations of this type have been ascribed to double reduction where a high degree of homology exists between corresponding sets of chromosomes as in the case of autotetraploids. Cadman (1942) in dealing with the reactions of cultivated potatoes to virus X found a reasonably consistent excess of recessives and concluded that the potato was probably autotetraploid in constitution. In the present case, however, similar excesses cannot be explained on the same basis for the plants concerned are indubitably complex hybrids and, consequently, cannot be strictly autopolyploids. Moreover, Howard and Swaminathan (1952), in an examination of meiosis in comparable triple hybrid material, observed that multivalents rarely occur.

Accordingly, it is probable that the unbalanced segregations /

segregations are due to the frequency of fusion of the different kinds of gametes. Apparently some degree of incompatibility exists between S. demissum on the one hand and S. Rybinii and S. tuberosum on the other, since hybridisations of these species are comparatively unprolific. Table 78 shows the average number of seeds per berry obtained from such hybrid and backcross matings. The fact that prolificacy increases after backcrossing to S. tuberosum indicates that factors contributing towards partial incompatibility are being eliminated, just as many of the "wild" characters introduced by S. demissum are being eliminated and replaced by the more desirable characters of cultivated varieties. Thus it is suggested that gametes possessing genes for blight resistance are at some disadvantage compared with their recessive competitors. Such differential affinity would result in the production of more susceptible seedlings than would be expected under conditions of complete compatibility. The excess would not be constant but would vary according to the genetical constitutions of the particular plants employed as parents.

TABLE 77.

COMBINED TOTALS (TABLES 20, 26, 30, 3, 4, 5, 6).

Expected R r	Observed R r	No. of Seedlings R	r	Total	χ^2	Deviation D.F.	P.
1 : 1	0·85 : 1	5994	7066	13060	87·99	1	Very Small
3 : 1	2·36 : 1	3162	1337	4499	53·40	1	Very small
15 : 1	10·14 : 1	598	59	657	8·36	1	Small
				18216			

TABLE 78.

FERTILITY IN HYBRID AND BACKCROSSED PROGENIES.

Cross	No. of Berries	No. of Seeds	Average No. of Seeds per Berry	Highest No. of Seeds per Berry
S. tuberosum × *S. demissum*	0	0	0·0	0
S. demissum × *S. tuberosum*	7	98	14·0	36
F_1 (*S. demissum* × *S. tuberosum*) × *S. tuberosum*	35	1172	33·5	70
2nd Backcross to *S. tuberosum*	23	1887	82·0	118
3rd Backcross to *S. tuberosum*	12	1673	139·4	210
S. demissum × *S. Rybinii*	0	0	0·0	0
S. Rybinii × *S. demissum*	1	1	1·0	1
F_1 (*S. Rybinii* × *S. demissum*) × *S. tuberosum*	8	12	1·5	3
Triple hybrid × *S. tuberosum*	20	1930	96·5	214
2nd Backcross to *S. tuberosum*	14	3447	246·2	377

These results are comparable with those reported by Stephens (1949) for selective elimination of the donor parent genotype in interspecific backcrosses involving Gossypium hirsutum and Gossypium barbadense.

On that basis it might be expected that the deviation in favour of recessives would tend to decrease with continued backcrossing to the cultivated type. Some indication that such takes place is apparent in the backcross ratios in progenies representing the 6th, 7th and 8th generations from the wild ancestor, S. demissum, which are set out in Table 79.

TABLE 79.

DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A.

Generation	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio
1st	Recessive x W.800(2)	902	1245	0.72:1
2nd	do. x 834c(29)	863	1101	0.78:1
2nd	W.967c(38) x Recessive	925	1119	0.83:1
2nd /				

TABLE 79 (CONTD.)

Generation	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio
2nd	Recessive x 833a(25)	161	173	0.93:1
2nd	835a(4) x Recessive	740	798	0.93:1
2nd	Recessive x 834b(6)	433	405	1.07:1
2nd	W.967c(38) x Recessive	925	1119	0.83:1
3rd	653c(35) x do.	295	344	0.86:1
3rd	764c(11) x do.	87	98	0.89:1
3rd	655(43) x do.	399	440	0.91:1

Seedling W.800(2) (Table 3), crossed with a recessive gave resistants and susceptibles in the proportion of 0.72:1 respectively. The seedlings selected from the progenies and used as parents, viz. 834c(29), W.967c(38), 833a(25), 835a(4) and 834b(6), all gave progenies showing a smaller deviation from the 1:1 ratio. Likewise seedlings selected as parents from the cross W.967c(38) x Recessive, viz. 653c(35), 764c(11) and 655(43), gave segregations more closely approaching 1:1 than the families from which they were selected. The differences which these ratios exhibit presumably reflect the relative extent of incompatibility still persisting in the parental forms. In later generations it is probable that ratios will approach the normal still more closely. Nevertheless, strictly normal ratios may seldom be obtained since blight resistance is essentially a demissum character and so long as it is retained, so also may be some residual incompatibility to upset the balance of segregations.

The /

The evidence for regarding differential compatibility of gametes as an explanation of the unbalanced segregations is supported by the widely different powers of seed production which potatoes exhibit together with the complete self- and cross-incompatibility so frequently encountered among species. Seed production varies between wide limits; the highest number recorded by the writer is 777 in one berry and the lowest 0, while most of the intermediate numbers may be found. In addition, most berries and particularly those from hybrid plants, contain a proportion of rudimentary seeds indicating that although fusion of gametes had failed, the stimulus was present. References to incompatibility in potatoes are numerous and some embody a wide range of results, e.g. Bukasov (1937) and Choudhuri (1944). In a study of the genetics of incompatibility Pushkarnath (1942) established 8 intra-sterile but interfertile groups of potatoes each possessing a different pair of 5 sterility factors which, operating in various combinations, controlled self- and cross-incompatibility.

The third type of deviation consisted of a large excess of resistant segregates. In the progenies concerned it was found that the resistant parent possessed two identical genes, presumably carried by two identical S. demissum chromosomes. If similar chromosomes of similar origin have a greater affinity for each other than S. demissum chromosomes have for their S. tuberosum counterparts, then unbalanced ratios amongst segregants would result. Such preferential pairing of chromosomes (i.e. partial auto-syndesis) would cause a greater proportion /

proportion than normal of the available R genes to be distributed in the progeny in the simplex condition, and a correspondingly smaller proportion to be inherited in the duplex state. Such a distribution of R genes would cause an increase in resistant segregates at the expense of recessives. In the experiments, preferential pairing was observed in two cases to reach approximately 50 per cent.

The occurrence of partial autosyndesis in interspecific hybrids may yield segregation ratios more or less typical of autotetraploid inheritance, as for example in the families bred from 1307a(23) (Table 45). This selection employed as pollen parent has the constitution R_3R_3, which, when crossed with recessives, gave a ratio of 7.80 resistants : 1 susceptible. Calculated as an autotetraploid the theoretical segregation would be 5:1 ($1R_3R_3$: $4R_3$: 1r) as compared with 3:1 for allotetraploid. Similarly in crossing R_3R_3 with R_3 types, the observed ratio of 12.83:1 is much closer to the autotetraploid 11:1 ($1R_3R_3R_3$: $5R_3R_3$: $5R_3$: 1r) than to the allotetraploid 7:1 ratio. Again the selfing of 1307a(23) resulted in a ratio of 28.85:1 which is a closer approximation to 35:1 (autotetraploid) than to 15:1 (allotetraploid).

Comparable results were obtained from 1512d(4) (Table 59) which was credited with the constitution $R_1R_1R_2$. In crosses with recessives a ratio of 7.20:1 was obtained which might be interpreted as an autotetraploid 5:1 ($1R_1R_1R_2$: $1R_1R_1$: $4R_1R_2$: $4R_1$: $1R_2$: 1r), the recessive and R_2 types being /

being susceptible to strain C. This is nearer to the observed ratio than the allotetraploid 3:1 ratio. In the double test (Table 60) the observed segregation 16 : 74 : 70 is also in closer agreement with the autotetraploid expectation 2: 5: 5 than with the allotetraploid 2: 3: 3 ratio.

The third example, 1306a(15) (Table 43) is less typical of autotetraploid inheritance. This plant, credited with the constitution $R_3R_3R_4$, gave on crossing with recessives a ratio of 8.99:1. On an autotetraploid basis the theoretical segregation would be 11:1 ($1R_3R_3R_4$: $1R_3R_3$: $4R_3R_4$: $4R_3$: $1R_4$: 1r), the recessive being the only type susceptible to strain B^1, while on an allotetraploid basis the theoretical ratio would be 7:1. The observed ratio is thus about midway between the two alternatives. In the double tests (Table 44) the theoretical segregations for an autotetraploid would be 1:1:10 for family 1433d and 2:5:5 for family 1431b, compared with 1:1:6 and 2:3:3 respectively for allotetraploid inheritance. The observed ratios fit neither closely and are again approximately midway between the two alternatives.

Thus, although segregations suggestive of autotetraploid inheritance have been obtained, they are limited in number and lack consistence. Autotetraploid inheritance implies completely random pairing between four homologues, a relationship which appears unlikely in interspecific hybrids involving three distinct species that can be intercrossed only with difficulty. Chromosome complements in the hybrids may consist /

consist of representatives of all three species. The frequency of pairing of any particular chromosomes at meiosis will depend upon the relative affinity existing between them and the segregation ratios will vary accordingly. It is not surprising, therefore, that wide variations in the distribution of characters in progenies occasionally occur and that inheritance in the potato is still not entirely free from controversy.

The fact that one or other of these deviations was in evidence in the majority of the progenies tested, illustrates their significance in the elucidation of the problem and in its practical application. No doubt they are the inevitable consequences of interspecific hybridisation, involving species that are not wholly compatible and have differences in chromosome number.

Having identified the genes and recorded their individual relationships to the different Phytophthora biotypes, it is interesting to review the early generations through which the genes had been transmitted. The triple hybrid lines provide evidence for this purpose, since all four genes were found in them. The original cross S. Rybinii x S. demissum produced one plant, Seedling 735, which, on crossing with three different varieties of S. tuberosum, gave rise to seven triple hybrid offspring. These are shown in Table 80 together with the genes accredited to them. Unfortunately two of the triple hybrids, 884(1) and 885(3), failed to survive long enough to be fully examined. It is unlikely, however, that they contained any new genes, since segregations in progenies bred from 735 indicate the presence of four genes only. /

only. The F_1 hybrid (735) may therefore be represented by $R_1R_2R_3R_4$ and S. demissum by the same genes in the homozygous condition.

TABLE 80.

GENES IDENTIFIED IN S. DEMISSUM, HYBRID 735 AND THE TRIPLE HYBRID SEEDLINGS.

S. demissum (CPC 2127)	$R_1R_1R_2R_2R_3R_3R_4R_4$
735 (*S. Rybinii* × *S. demissum*)	$R_1R_2R_3R_4$
884(1) (735 × *S. tuberosum*)	R_1R?
885(1)	R_1
(2)	R_1R_3
(3)	R_3R?R?
(4)	$R_1R_3R_4$
886(1)	R_2R_4
(2)	R_1

The distribution of four independent genes in the 72 chromosome species S. demissum is not clear. The basic chromosome number in potatoes has long been the subject of controversy, and although widely accepted as 12, universal agreement has still to be reached. If 12 is the true basic number, and S. demissum chromosomes consist of 3 diploid sets of 24, one of these sets must have resistance genes in more than one pair of chromosomes. The presence of four R genes in the F_1 and three in triple hybrid plants precludes the postulation of an allelomorphic association of two R genes for the purpose of limiting resistance factors to three pairs of chromosomes.

As previously indicated, the effect of the major genes is not absolute. Their fundamental role is to determine the general reaction, resistance or susceptibility, but the phenotypic /

phenotypic expression may be modified by unidentified minor factors which control the degree of resistance in the presence of major genes, and the degree of susceptibility in the absence of such genes. The classification of seedlings into two groups, resistant and susceptible, presents no serious difficulty provided the necessary care is taken to maintain the vigour of the plants and to ensure that each is properly inoculated. No evidence has been found which suggests that minor genes alone can induce a hypersensitive condition in the plant or are capable of inhibiting the expression of major genes. According to Petterson (1941), foliage resistance may be divided into nine groups ranging from highly resistant to highly susceptible. Detached leaves under very humid conditions were employed for the test. The various groups observed presumably represent degrees of resistance and degrees of susceptibility resulting from the action of different minor gene complexes in the material. The partial resistance observed in the variety President (Stevenson, Schultz, Akeley and Cash, 1945) is caused by minor genes, since the variety is not hypersensitive and possesses no major genes.

It should be emphasised that the resistance referred to in the present experiments is foliage resistance, since the reactions of different parts of the plant need not necessarily be identical. Tests of young seedlings revealed that resistant leaves and susceptible cotyledons may occur in the same plant. In such cases the reaction of the cotyledons /

dons must be ignored in order to classify accurately a crop plant which is normally vegetatively reproduced. Examination of tubers of the different genotypes showed that, in a general sense, tuber resistance tended to follow leaf resistance although it was usually weaker and less consistent. Different varieties possessing the same R gene showed considerable variation in depth of penetration by the common strain of the fungus, indicating that minor genes exert a significant effect in tuber resistance. In tubers of each of the four genotypes R_1, R_2, R_3 and R_4 it was possible by graft inoculation to obtain a deep penetration of the tissues by each of seven strains of the parasite. In a few exceptional cases the entire tubers were quickly discoloured by a strain to which the leaves were fully resistant, but sporulation in such cases was sparse or absent. On the other hand, strain F showed a pronounced lack of vigour on tubers of Craigs Royal, a variety of S. tuberosum, although it quickly engulfed those of an R_3R_4 resister, i.e. resistant to strains A, B^1, B^2, C, D, E, G and H. Differences in the speed of reaction of different parts of the plant have been reported by Müller (1950). He found the reaction to be quickest in young sprouts and leaves, slow in the inner parenchyma of stems, and very slow in petals and the parenchyma of tubers. It is probable that the greater variation in tuber resistance is due to the greater influence of minor resistance factors in organs which react relatively slowly. Differences in the reaction of tubers of susceptible varieties which were observed /

served by de Bruyn (1943) may also be ascribed to the effect of minor genes.

Bonde, Stevenson and Clark (1940) found that tuber resistance and leaf resistance occurred together in a high percentage of cases, but suggested that the two characters may not be controlled by the same genetic factors. Some years later, however, Montaldo and Akeley (1946) demonstrated a definite positive correlation between leaf and tuber resistance. A few exceptions occurred, but these were considered too small in number to invalidate the + correlation.

The research work of Müller and his collaborators (e.g. Müller, Meyer and Klinkowski, 1939; Müller, 1941; Müller and Boerger, 1941; Müller and Behr, 1949; Müller, 1950) on the physiology of resistance led to the conclusion that resistance genes act as accelerators of a defence reaction which susceptible genotypes are also capable of producing. The genes are not responsible for the resistant condition itself, but merely induce a genetic predisposition of the tissues to acquire a local immunity from infection when brought into contact with parabiontic races of the parasite. Thus the reaction speed in resistant genotypes is relatively fast while in susceptibles it is relatively slow. These and other conclusions reached from the physiological aspect provide an understanding of the nature of resistance and of the functions of the genes, without conflicting in any way with the genetic interpretation of the problem.

Changes /

Changes in the infective power of Phytophthora infestans have been recorded by several investigators. Reddick and Mills (1938) and Reddick (1940) found an increase in virulence after the fungus had completed several passages through varieties which were partly resistant to the original form. This increased virulence remained unreduced even after continuous culture for 20 generations on ordinary susceptible varieties. Reddick considered that the greater virulence could be induced at will by culture on partial resisters, but this opinion was not confirmed in experiments by Bonde, Stevenson and Clark (1940).

Investigations comparable with those of Reddick and Mills were carried out by de Bruyn (1947) using single spore cultures. She found that certain strains which normally parasitised potatoes became adapted to tomatoes after several passages through them, and that the new strains retained their powers of attacking tomatoes after further culture on potatoes. She regarded the fungus as very plastic and adaptable, and attributed changes in pathogenicity either to modification of the fungus or to selection of strains.

The exact mode of origin of specialised strains remains obscure. In P. infestans several possibilities exist since sexual reproduction, although apparently rare, can occur (Clinton 1911) and the hyphae are aseptate and multinucleate. No doubt, limited modification without nuclear /

nuclear change can take place, resulting in quantitative differences in vitality and aggressiveness. But such modification cannot account for the qualitative differences between the strains examined. If differences were quantitative only, then specialised strains, having a wider host range, would be more virulent and would cause greater damage to varieties of S. tuberosum than the common strain. The reverse has been found to be true. Qualitative changes appear to be associated only with changes in the genetic constitution of the organism. If P. infestans is heterokaryotic, as is likely to be, such new strains could arise by nuclear association or dissociation. Even single zoospore cultures could quickly lose their uniformity by mutation and so provide a means for the selection of new strains. Although adaptation is reversible, as shown by de Bruyn (1951) the phenomenon could be interpreted as the result of the selection of mutant nuclei. The failure to accomplish adaptation, reported by Müller (1935), Bonde, Stevenson and Clark (1940) and encountered in the present experiments, indicates that the fungus cannot always be modified at will and that factors other than environmental are concerned in parasitic specialisation in P. infestans.

Whatever the fundamental basis of specialisation may be, it is clear that the strains which become established are those specially adapted to the varieties grown. Being so adapted, they are more prolific on their natural host plants than any other strain and must, therefore, be expected to differ in their reproductive capacity on

varieties of S. tuberosum. It was found that strains with the widest host range were least prolific on S. tuberosum and consequently tended to die out at an early stage in competition with less specialised forms. The known strain with the widest host range, viz. F, was found to penetrate tubers of S. tuberosum only slightly and the diseased tissue was limited to the regions round the points of inoculation. Seven months after inoculation, affected tubers bore strong sprouts and later produced healthy plants. By comparison, tubers of genotype R_3R_4 treated in the same fashion were completely diseased within one month. Since strain F is so ineffective against S. tuberosum, it is likely that the hypothetical strain (1,2,3,4), should it ever arise, would be even less pathogenic on the same variety.

Specialised strains have frequently been described as more virulent than the common strain because they have a wider host range. It is clear that as strains they are not necessarily more virulent but, in fact, are less virulent in relation to varieties of S. tuberosum. The term "virulence" is thus applicable only in comparisons which refer specifically to a particular type of host plant.

A universal scheme for the classification and nomenclature of specialised strains of Phytophthora infestans would be extremely helpful, not only in appreciating the work of other investigators, but also in planning a breeding programme for the immediate future. In the past, each

investigator /

investigator has independently built up a differential host series and designated strains of the fungus according to his particular fancy. By means of an exchange of differential host varieties between Mastenbroek in Holland, Reddick and Peterson in the U.S.A., and the writer, an attempt has been made to compare the genetic constitutions of the differential hosts and the pathogenicity of the strains of the parasite in the three countries. The results indicate that the Dutch and American varieties have in their constitution only genes already known in this country and that the Dutch and American strains of Phytophthora fit the general scheme of classification herein devised.

In a vegetatively reproduced parasitic organism such as P. infestans which is liable to modification in an environment other than that of its natural host, the most satisfactory method of classification appears to be one based upon the genetic constitution of the host. It is the selective influence of the host that determines which strain shall prevail and consequently the pathogenicity of a new strain is predetermined by the host genotype. The relationships between genes and strains could not be ascertained in the early stages of the work because the identification of the genotypes had to await the arrival of strains and the latter could not themselves be differentiated without a suitable range of hosts. Specialisation in the parasite is thus directly dependent upon the progress of plant breeding.

Investigations /

Investigations have now reached a stage, however, when genes and strains can be correlated and the pattern of these relationships formulated.

In presenting the table of relationships between genes and strains, it is fully realised that, although only four major genes have been distinguished in an extensive search of breeding material, it is possible that other genes may be discovered. The advent of additional genes would, in all probability, greatly increase the number of identifiable strains. Nevertheless, the scheme of relationships between the known genes and strains form a pattern which may readily be extended should the need arise.

In the present scheme, it is possible to distinguish sixteen strains by employing only five host plants. The limits of specialisation in the parasite are unknown but even although differentiation may be potentially very great, the number of strains of practical significance is limited by the number of genetically different host varieties available. In earlier investigations, Lehmann (1937, 1938) distinguished eight strains, although fifty plants were employed in the tests. Müller (1950) on the other hand, claimed that he could distinguish thirty-one strains but he depended upon tuber tests as well as foliage tests for the purpose. Presumably, minor gene effects in the tubers are more clearly expressed than in the foliage and assisted in the determination of minor differences in the isolates. Some of these strains, supplied by Dr. Müller, were tested on the foliage of /

of the present differential host series but no differences between certain cultures were detected. This host series, which is based on major gene differences as expressed in the foliage, is essentially concerned with major differences between strains or populations of the parasite. Accordingly, the sixteen strains referred to may be more accurately described as sixteen groups of variants within each of which only minor differences exist. For more detailed comparisons of isolates it is necessary to supplement with tuber tests.

The continued appearance of specialised strains provides a serious problem for the practical plant breeder in search of commercial results. Not only can plants possessing one R gene be attacked, but combinations of three different R genes are also vulnerable. The possibility of specialisation reaching its limit at that point cannot be overlooked and breeders must, therefore, aim at the combination of all four genes. It is true that certain lesser combinations of genes have so far provided adequate protection but it is unlikely that they will continue to do so. In the event of the discovery of further and more powerful genes, the position would be fundamentally altered.

A factor which may have some bearing on the problem is the effect of climatic conditions on the vigour and reproductive powers of specialised strains. It is well known /

known that strains of rust in cereals are associated with particular climatic areas. If climatic preferences are well defined in Phytophthora strains, it may be possible to distribute varieties according to genetic constitution to the areas where they would be least vulnerable. Investigations on that aspect of the problem may yield valuable results.

In the event of the failure of hypersensitivity as an effective form of resistance, progress can still be made by breeding for the most favourable combinations of minor genes. The resistance so obtainable is only relative but, on the strength of the available evidence, it has the advantage of remaining equally effective against all the known specialised strains that have arisen during the search for hypersensitive varieties.

SUMMARY.

1. The common strain and nine specialised strains of Phytophthora infestans were employed in testing seedlings and seedling progenies, obtained from four different breeding systems, for resistance to the disease.

2. The resistance exhibited by S. demissum (CPC 2127) and seedlings bred from it is due primarily to the hypersensitive condition of the protoplasm. This condition is manifested in the presence of one or more major resistance genes, of which four have been identified, viz. R_1, R_2, R_3 and R_4.

3. Each major gene confers resistance to the common strain and to a particular group of specialised strains of the parasite. The genes are inherited independently in simple Mendelian fashion.

4. A series of minor genes, associated with morphological and physiological characters of the plant, modify the phenotypic expression of the major gene system, and so determine the degree of susceptibility in susceptible phenotypes and the extent of necrosis in resistant ones.

5. In the early generations of S. demissum-S. tuberosum hybrids, the irregularity of chromosome behaviour and the presence of unpaired chromosomes caused the ratios of resistants /

resistants to susceptibles to vary widely from standard Mendelian ratios.

6. In certain progenies, particularly those obtained by crossing S. tuberosum plants with resistant hybrid derivatives of S. demissum, deviations from standard Mendelian ratios were consistent in their trend, and appeared to be due to some relationship between genes affecting disease resistance and incompatibility genes.

7. In certain parent seedlings with duplicate genes, derived from self-fertilised plants or from recombination crosses, partial auto-syndesis resulted in an excess of resistant segregates in the progenies.

8. The interrelationships of ten strains of blight (Phytophthora infestans) and four major genes R_1, R_2, R_3 and R_4 controlling resistance to the disease in the potato are examined.

9. Since dominance of the genes is complete the maximum number of phenotypic reactions which can be distinguished is sixteen. This series represents the complete range of differential hosts for the material in question and is capable of distinguishing sixteen different strains of the parasite.

10. The reactions exhibited by the series form a concise statement /

statement of the various relationships and provide the necessary groundwork for the systematic classification of strains. The classification will afford a basis for the calculation of segregation-ratios to be expected from the mating of any pair of genotypes when infected with any strain or group of strains of the parasite.

11. Each specialised strain, being adapted to a particular Solanum genotype, is more prolific on it than on any other. This genotype is regarded as the natural host of the strain.

12. Specialised strains differ in their effect upon varieties of S. tuberosum: Those with the widest host range being least virulent. Also, they are less prolific and cause less damage than the common strain.

13. The exact mode of origin of strains is not clear but mutation appears to play a significant part.

14. Specialisation appears to progress in stages in certain directions determined by the genetic constitution of the various hosts. Examples of three progressive stages of specialisation are apparent in the material reported on here. If the fourth stage should be reached, the resulting strain will be capable of attacking all sixteen genotypes.

15. It is suggested that strains should be classified according to the genetical constitution of their natural hosts and that each should be known by the numeral pertaining to the genes in question.

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IV.—Inheritance of Resistance to Two Strains of Blight (*Phytophthora infestans* de Bary) in Potatoes.

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Introduction

The existence in Mexico of blight-resistant species of potato has been known for many years, but they occur in the wild and are quite unsuitable for agricultural purposes. In order to utilise their resistance to disease it is necessary to combine disease resistance with the cropping qualities of cultivated forms while eliminating the undesirable characters which are prominent in the wild forms. Breeding work with this object in view has been in progress at the Scottish Plant Breeding Station for several years, and results obtained in the course of testing progenies for reaction to blight infection are discussed in the following pages.

Perusal of the literature shows that much breeding work has been done in several countries, and that the species *Solanum demissum* Lindl. has most frequently been employed as the source of resistance genes. Nevertheless, precise evidence of the mode of inheritance of resistance is scarce, due probably to the occurrence of biotypes of *P. infestans* and to the different polyploid chromosome complements possessed by *S. demissum* and *S. tuberosum.*

The cyto-genetical basis of inheritance in the tuber-bearing Solanaceæ has not been definitely established. Earlier work was interpreted to indicate that the potato behaved as a diploid. Investigations of New World potatoes, following the first Russian expedition to South America in 1925, established the well-known polyploid series into which potatoes are now grouped. Müller (1930) put forward genetical evidence of polyploid inheritance in potatoes from experiments on breeding blight-resistant seedlings. Later, Lunden (1937) offered a considerable amount of data on the inheritance of characters in varieties of *S. tuberosum* and suggested an auto-tetraploid basis. Cadman (1942) also explained results concerning the inheritance of reaction to virus X in a similar fashion.

Although the polyploid nature of the potato family has been appreciated for some time, the basic chromosome number, frequently accepted as 12, has been the subject of speculation. Some definite indications that the basic chromosome number is less than 12 has been brought to light by the work of Müntzing (1933), Ellison (1936 *a*), and Choudhuri (1943). In cytological investigations of cultivated varieties and wild species, including representatives of the 24, 36, and 48 chromosome groups, they observed secondary associations at meiotic metaphase which led them to conclude that the basic chromosome number in potatoes was probably 6. This opinion was also supported by Emme (1936) in explaining the results of a cross between a 48- and a 24-chromosome species. She obtained a 36-chromosome hybrid showing 18 units at first metaphase, and a more or less regular disjunction of the 18 partners. This should not occur with a basic number higher than 6.

Evidence is also available supporting the view that cultivated varieties are allopolyploids. Meurman and Rancken (1932) and Ellison (1935) found that somatic cells of certain varieties of *S. tuberosum* possessed not more than two satellite-carrying chromosomes. Sepeleva (1937) made a classification of *S. tuberosum* chromosomes and found irregular numbers of pairs of the various morphological types, some being represented by only one pair. That the cultivated potatoes are of mixed origin was also suggested by Juzepczuk and Bukasov (1929) as a result of a survey of the geographical distribution of species, and by Longley and Clark (1930) in cytological investigations of cultivated varieties.

In consideration of the above evidence, the basic chromosome number of potatoes is tentatively accepted as 6, *S. tuberosum* being regarded as an octoploid and *S. demissum* as a dodecaploid in the following analysis of the inheritance of resistance to blight.

The existence of biotypes of *P. infestans* differing in the virulence of their attack on members of the genus *Solanum* is now generally accepted, but the origin of these physiological forms is not clear. The isolation of biotypes has been reported, particularly in Germany where two physiological forms were employed by Schick (1932), four by Schick and Schaper (1936) and Schick and Lehmann (1936), and eight by Lehmann (1937, 1938). In their experiments, these authors were able to distinguish between the various biotypes by the reactions of certain wild Solanums and hybrid seedlings to infection with them.

In Britain, O'Conner (1933) isolated two distinct strains of blight which she designated A and B respectively. Seedlings bred from *S. demissum* were resistant to strain A, the commoner one, but were susceptible to the more virulent and rarer strain B. In further experiments with these strains Salaman (1941) found that resistant seedlings could be divided into two groups, viz. "single resisters" and "double resisters," the former being resistant only to strain A, but the latter resistant to both strains.

According to Reddick and Crosier (1933) no biotypes have been observed in North America. By distributing to Russia and Germany tubers of plants exhibiting different degrees of resistance and comparing the results of infection, they found that American cultures of *P. infestans* gave the same reactions as local cultures at Moscow in 1928 and at Munich in 1930. Reddick and Mills (1938) obtained oospores in cultures of European and Australian origin but none from local cultures. They were able, however, to "step up" the virulence of a local culture by passing it through a series of potato varieties, each variety in turn being known to possess a successively higher degree of resistance than the previous host, until a point was reached where a number of hybrids which had originally been immune from the fungus were severely affected. They considered that the fungus was to some extent "plastic" and that its virulence could be modified by appropriate treatment.

It may be assumed, however, that there exists a common or original form of blight widely distributed in Europe and North America, and that the various biotypes referred to have arisen from it.

Müller (1941) concluded that resistance was conferred on an infected plant by its production of a substance toxic to the development of the fungus. He considered that resistant plants produced this substance quickly after penetration of the fungus, but that susceptible varieties produced the toxin at too late a stage of infection for it to be effective. Plants may also acquire immunity from a strain to which they are normally susceptible by prior infection with a strain to which they are resistant (Müller and Börger, 1941). Presumably a toxic substance resulting from the first infection prevented the second. Müller and Börger subsequently concluded that resistance genes function only as accelerators of toxin production by the plant.

Puskarev (1937) found that a number of varieties of *S. demissum* were resistant to blight when infected with zoospores, but when infected by a "special method" none of the varieties was resistant, not even those indicated by Schick to be resistant to all Phytophthora races. On the basis of Müller's conclusions this phenomenon seems to imply that the "special method" of infection has the effect of speeding-up the establishment of the fungus within the host and that the rate of production of the toxic substance has remained constant. If so, the plant may be regarded as consistent in its reaction despite any change in the virulence of the parasite or in the circumstances of infection.

The available evidence therefore indicates that *P. infestans* is stable under normal conditions but more or less plastic under treatment; that biotypes may arise although the circumstances of their origin are unknown; and that the reaction of the plant to the disease is under genetical control.

Materials and Methods

Three potato species were employed in the investigations, viz. *S. demissum* Lindl., a blight-resistant Mexican species ($2n=72$); *S. Rybinii* Juz. et Buk., a blight-susceptible South American species ($2n=24$); and *S. tuberosum* L., a blight-susceptible species represented by various cultivated varieties ($2n=48$).

The species *S. demissum* consists of a number of different varieties. Lehmann (1941) found that some were resistant and some susceptible to his two races of *Phytophthora*. In crosses between resistants and susceptibles all F_1 plants were resistant, and the results of F_2 and backcrossed progenies showed resistance to be conditioned by a single Mendelian gene. The original resistant varieties would thus be homozygous resistants. In addition to homozygous forms the species contains a number of heterozygous varieties (Schick and Schaper, 1936, and Puskarev, 1937).

The variety of *S. demissum* used in the present experiments conforms with the description of f. *tlaxpehualcoense* Buk. It proved to be highly fertile and the chromosome behaviour at meiosis was normal and regular. No segregation was observed on selfing.

In the cross- and self-pollinating operations all the female flowers were protected against contamination with foreign pollen except in those parents, marked N.S. in Table VIII, where natural berries were utilised.

Two strains of *P. infestans* were employed in the work and have been designated A and B. Strain A was local in origin and was presumed to be the common strain previously referred to, since cultures taken from various

localities in Scotland gave the same reactions. Strain B was much more virulent and was acquired by maintaining a field sample of the A strain during winter on a mixed population of resistant and susceptible seedlings until one of the hitherto resistant plants became affected. It was then isolated and cultured on plants known to be unaffected by the A strain.

The experimental progenies were tested during the seedling stage in glass-houses. Cultural conditions advocated by Crosier (1933) were employed as a basis for adapting the premises to meet the requirements of the test. Optimum conditions of temperature and humidity for successful infection were attained by means of adjustable heating and ventilation, external sun shades and an abundant water supply.

After being thoroughly wetted the seedlings were sprayed with a spore suspension of the fungus. Three successive applications at approximately 12-hour intervals were made to ensure that all plants were thoroughly infected. The susceptible plants were killed within seven days and the resistants were then transplanted and grown to maturity. The term "resistant" has been adopted rather than "immune" and describes plants which remained free from the disease after seven days' treatment.

Various tests confirmed that the stage of growth of the plant has no effect upon its reaction to blight infection, a fact which has also been observed by Pethybridge (1910), Müller (1930), Beaumont (1934), Crosier (1934), and Mills (1938).

The efficiency of the test has been confirmed over several years by the freedom from disease in the field of those seedlings which had survived the glass-house test. Parallel tests of second-year progenies were carried out in the field and under glass in order to compare the effect of the two environments. The results were identical in seasons when weather conditions favoured the natural spread of blight. It is evident that field tests depend upon climate, while the efficiency of the glass-house method depends only upon careful technique.

Experimental Results

(a) *S. Rybinii–S. demissum–S. tuberosum* Hybrids

In order to avoid the complications of irregular chromosome numbers which are a feature of hybrids between *S. demissum* ($2n=72$) and *S. tuberosum* ($2n=48$), attempts were made to synthesise a blight-resistant hybrid which would have the same number of chromosomes as *S. tuberosum* and would cross readily with it. Accordingly *S. demissum* pollen ($n=36$) was applied to a large number of *S. Rybinii* flowers ($n=12$) and eventually a berry containing one seed was obtained. This seed germinated to produce a self-fertile plant in which 48 somatic and 24 gametic chromosomes were observed. This plant (Ref. No. 735) was thereupon crossed with *S. tuberosum* varieties. The cross was not prolific but 8 berries were obtained, yielding a total of 12 seeds, 7 of which germinated. These triple hybrids were self-fertile and were readily backcrossed to *S. tuberosum*. Seedlings derived from the first backcrossed and subsequent generations proved to be highly fertile and prolific. In crossing with *S. tuberosum* they could be used either as male or female parent, and their utilisation has helped to overcome the sterility handicap in potato breeding.

The seedlings referred to above were tested for resistance to both the A and B strains of blight. Segregations obtained in the various progenies are shown in Table I. *S. Rybinii* was susceptible to both strains while *S. demissum* and the hybrid (No. 735) were resistant to both. The segregations observed in subsequent progenies showed that a definite relationship existed between the reactions to the two strains of blight. In order to examine this relationship certain progenies were retained until the second year and planted in duplicate. One series was infected with the A strain, the other with the B, and the results demonstrated the presence of three different phenotypes, viz.:

(1) Plants susceptible to both A and B.
(2) Plants resistant to A but susceptible to B.
(3) Plants resistant to both A and B.

Since no plant was found to be susceptible to A and resistant to B, these facts suggest that resistance may be controlled by two factors Ra and Rb which confer resistance at the level of the A and B strains of blight respectively. Plants carrying the Ra gene are resistant to the A strain alone, while plants carrying the Rb gene are resistant to both strains.

In crossing *S. Rybinii* ($n=12$) with *S. demissum* ($n=36$) it may be presumed that 12 *Rybinii* chromosomes paired with 12 from *demissum* and that the remaining 24 *demissum* chromosomes paired amongst themselves. Thus 12 autosyndetic and 12 allosyndetic bivalents would be formed in a manner similar to that observed by Ellison (1936 *b*) in other *Solanum* hybrids.

When the hybrid 735 was crossed with *S. tuberosum* all the offspring were found to carry the Ra gene, but only some of them the Rb gene. In view of the ratios obtained and assuming potatoes to be allopolyploids with a basic chromosome number of 6, *S. Rybinii* may be represented by $ra_1ra_1rb_1rb_1$ and *S. demissum* by $ra_1ra_1Ra_2Ra_2Ra_3Ra_3Rb_1Rb_1rb_2rb_2Rb_3Rb_3$, where the suffixed numbers differentiate the factor pairs concerned. On that basis the hybrid 735 would be constituted $ra_1ra_1Ra_2Ra_3rb_1Rb_1rb_2Rb_3$, in which Ra_2 pairs with Ra_3 and rb_2 with

Rb_3 in absence of their normal partners. Self-fertilisation of 735 should therefore give a progeny consisting entirely of resistants under A strain infection and should segregate in the ratio of 15 resistants to 1 susceptible under B strain infection (Ref. No. 897 in Table I).

TABLE I

Ref. No.	Parentage	A Strain No. of Seedlings R	A Strain No. of Seedlings r	A Strain Theoretical Ratio	B Strain No. of Seedlings R	B Strain No. of Seedlings r	B Strain Theoretical Ratio	Suggested Genotypes (Dominant Genes only)
735	*S. Rybinii* × *S. demissum*	1	0	∞ : 0	1	0	∞ : 0	Recessive * × $Ra_2Ra_2Ra_3Ra_3Rb_1Rb_1Rb_3Rb_3$
897	735 selfed	71	0	∞ : 0	63	1	15 : 1	$Ra_2Ra_3Rb_1Rb_3$
994	735 × *S. Rybinii*	16	0	∞ : 0	14	2	3 : 1	$Ra_2Ra_3Rb_1Rb_3$ × Recessive *
884–6	735 × *S. tuberosum*	7	0	∞ : 0	5	2	3 : 1	$Ra_2Ra_3Rb_1Rb_3$ × Recessive †
995	884(1) × *S. tuberosum*	21	6	3 : 1	12	15	1 : 1	Ra_xRb_1 × Recessive †
996	885(1) × do.	94	99	1 : 1	0	73	0 : ∞	Ra_x × Recessive †
997	885(2) × do.	216	75	3 : 1	125	124	1 : 1	Ra_xRb_3 × Recessive †
998	885(3) × do.	114	19	7 : 1	121	44	3 : 1	$Ra_xRb_1Rb_3$ × Recessive †
1112	885(3) selfed	..	..	..	54	4	15 : 1	$Ra_xRb_1Rb_3$
1104	885(4) × *S. tuberosum*	..	..	..	78	33	3 : 1	$Ra_xRb_1Rb_3$ × Recessive †
1015	885(4) selfed	187	5	63 : 1	31	0	15 : 1	$Ra_xRb_1Rb_3$
999	886(2) × *S. tuberosum*	39	36	1 : 1	0	52	0 : ∞	Ra_x × Recessive †
1016	886(2) selfed	42	16	3 : 1	0	18	0 : ∞	Ra_x
1116	1015*a*(1) selfed	..	..	..	58	0	∞ : 0	$Ra_xRa_xRb_1Rb_1Rb_3Rb_3$?

The female parent is named first throughout.

* The full recessive genotype of *S. Rybinii* is $ra_1ra_1rb_1rb_1$.

† The full recessive genotype of *S. tuberosum* is $ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2$.

When hybrid 735 is crossed with varieties of *S. tuberosum*, which may be represented by $ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2$, the triple hybrid offspring would be of four types, viz.:

(1) $ra_1ra_1ra_2Ra_xRb_1rb_1rb_2Rb_3$,
(2) $ra_1ra_1ra_2Ra_xRb_1rb_1rb_2rb_3$,
(3) $ra_1ra_1ra_2Ra_xrb_1rb_1rb_2Rb_3$,
(4) $ra_1ra_1ra_2Ra_xrb_1rb_1rb_2rb_3$,

and under A strain infection would be wholly resistant, while under B strain infection would segregate in the proportion of 3 resistants to 1 susceptible. The symbol Ra_x is used in place of Ra_2 and Ra_3 since random distribution would prevent their identification. The second and third of the above genotypes cannot be distinguished by their segregations, but three of them and possibly all four are represented in the 6 triple hybrids included in Table I. These triple hybrids 884(1), 885(1), 885(2), 885(3), 885(4), and 886(2) were all backcrossed to *S. tuberosum* (Ref. Nos. 995, 996, 997, 998, 1104, and 999 in Table I). The resulting segregations made it possible to group them under their respective genotypes as follows:—

Genotype 1, 885(3), 885(4),
„ 2 or 3, 884(1), 885(2),
„ 4, 885(1), 886(2),

and the combined segregations are analysed and compared in Table II. The approximation to the theoretical expectation is close.

TABLE II

Parentage	A Strain Infection Expected	A Strain Infection Observed R	A Strain Infection Observed r	A Strain Infection P	B Strain Infection Expected	B Strain Infection Observed R	B Strain Infection Observed r	B Strain Infection P
Genotype 1 × Recessive	7 : 1	114	19	0·8–0·7	3 : 1	199	77	0·3–0·2
Genotype 2, 3 × Recessive	3 : 1	237	81	0·8	1 : 1	137	139	0·9
Genotype 4 × Recessive	1 : 1	133	135	0·9	0 : ∞	0	125	1·0

The two triple hybrids belonging to genotype 1 and one belonging to genotype 3 were self-fertilised. Each progeny showed segregations consistent with the factorial constitution assigned to it (Ref. Nos. 1112, 1015, and 1016 in Table I). A second selfed generation from the triple hybrid 885(4) was examined with the B strain only and all the plants proved to be resistant (Ref. No. 1116 in Table I).

A further differentiation of the Ra and Rb genes may be made. Five progenies comprising 378 seedlings obtained by cross- or self-fertilisation of plants resistant to the A strain of blight were tested with the B strain and all were susceptible. Consequently two doses of the Ra gene are insufficient to attain resistance on the Rb level and it is doubtful if such a resistance can be built up by a concentration of Ra genes.

(b) *S. demissum–S. tuberosum* Hybrids

A series of breeding experiments were conducted with the object of producing blight-resistant seedlings of economic value from the two species *S. demissum* and *S. tuberosum*. In this work, the progenies were tested only with the A strain of blight, but a number of incidental tests were made with the B strain to confirm the presence or absence of the Rb gene.

S. demissum, used as female parent, was successfully crossed with pollen of cultivated varieties of *S. tuberosum*. All attempts to effect the reciprocal cross failed. The F_1 plants were only partially self-fertile, and several small F_2 families which were obtained did not provide satisfactory data for genetical analysis. A few resistant F_2 segregates were, however, used for further breeding.

The variety of *S. demissum* employed was the same as in the previous experiments. The F_1 progenies obtained by crossing it with *S. tuberosum* were resistant to both strains of blight. Various backcrossed progenies ($F_1 \times$ *S. tuberosum* var. Alness) were tested with the A strain of blight and the results are shown in Table III.

TABLE III

$F_1 \times$ Susceptible

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
429*a*(1) × *S. tuberosum*	861, 938	61	22			
429*a*(4) × do.	862, 939	43	15			
429*a*(6) × do.	940	45	14			$Ra_2(Ra_3)$ $Rb_1(Rb_3)$ × Recessive *
429*a*(8) × do.	864	54	16			
do. × do.	736	67	26			
do. × do.	941	98	16			
429*b*(5) × do.	738	77	18			
	Total	445	127	3·5 : 1	> 3 : 1	

* Recessive = $ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2$.

The observed ratios proved to be slightly inconsistent, but the totals gave a ratio of approximately 3·5 resistants to 1 susceptible. The results obtained by Reddick (1934) using the strain of blight prevalent in the U.S.A., presumably equivalent to the A strain used here, were very similar.

The theoretical backcross ratio, however, can hardly be calculated. The F_1 hybrids had 60 chromosomes and their behaviour at meiosis was irregular. Salaman (1928) found in the F_1 from similar parentage 24 bivalents and 12 univalents, and frequently one or more univalents were displaced at metaphase and appeared to lie outside the spindle. Becker (1939) also observed considerable irregularities at meiosis, including frequent non-orientated and lagging chromosomes.

In the experiments of Puskarev (1937) the F_1 hybrids between *S. demissum* and *S. tuberosum* had 60 chromosomes, but in backcrossed plants the numbers ranged from 50 to 60. The pollen grains of the male parent carried 24 chromosomes, therefore the numbers in the female gametes of the F_1 must have ranged from 26 to 36, showing a loss of univalents up to 10.

It has been observed that plants closely resembling the cultivated parent have fewer chromosomes than those exhibiting many characters of the wild form. Salaman (1928) found that derivatives of *S. demissum* × *S. tuberosum* which had 6–12 univalents approached the wild parent in general type, while those with less than 6 univalents resembled *S. tuberosum* more closely. These observations indicate that genes for the wild characters are carried by the univalent chromosomes. That genes for all the characters distinguishing the two species are carried by the unpaired *demissum* chromosomes is unlikely since blight-resistant plants with only 48 chromosomes have been obtained. However, it is apparent that many typical *demissum* characters are controlled by genes in the univalents,

and if chance determines the frequency of the univalents in the offspring, the resulting segregations will vary accordingly.

The work of McClintock and Hill (1931) and others has shown that when a bivalent and a univalent are formed instead of a trivalent, the univalent may or may not be included at the first and second divisions. If it is lost in the cytoplasm through not being included on the spindle, the number of X gametes will be increased at the expense of the X+1 gametes.

In backcrossing the F_1 to *S. tuberosum* it appears that as many as 10 of the 12 univalents are liable to be lost. Consequently genes for resistance to blight are likely to disappear and the number of susceptible segregates in the progeny will be increased at the expense of the resistants. The frequency with which the univalents carrying genes for blight resistance are included in the nucleus will affect the proportions of resistant phenotypes obtained, and this will therefore be greater than the theoretical output of the paired chromosomes.

Considering the constitutions previously applied to *S. demissum* ($ra_1ra_1Ra_2Ra_2Ra_3Ra_3Rb_1Rb_1rb_2rb_2Rb_3Rb_3$) and *S. tuberosum* ($ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2$), the F_1 would be represented by $ra_1ra_1Ra_2ra_2(Ra_3)Rb_1rb_1rb_2rb_2(Rb_3)$, in which the Ra_3 and Rb_3 genes are contained in univalents.

If, in backcrossing the F_1 to *S. tuberosum*, the genes for blight resistance are lost, then the theoretical ratio in the progeny would be 3 resistants to 1 susceptible and the four genotypes would be:

$$ra_1ra_1Ra_2ra_2Rb_1rb_1rb_2rb_2,$$
$$ra_1ra_1Ra_2ra_2rb_1rb_1rb_2rb_2,$$
$$ra_1ra_1ra_2ra_2Rb_1rb_1rb_2rb_2,$$
$$ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2.$$

This ratio, however, would undoubtedly be upset by the presence of some univalents carrying effective genes. In the event of no loss of genes the theoretical ratio would be 15 resistants to 1 susceptible. The observed ratio of approximately 3·5 : 1 contains fewer resistants than one might expect and suggests that resistance-carrying univalents have largely been lost.

The segregations obtained in second backcrossed progenies are shown in Table IV. The three resistant seedlings used as parents gave distinctly different ratios in their progenies. Three different genotypes are therefore involved, since the male parents are all recessive. The ratios, however, show some deviation from normal Mendelian segregation and these deviations may again be explained by the presence of univalent chromosomes. In a cytological examination of one of the parents, 556*a*(30), 53 chromosomes were counted in a root-tip preparation. The presence of a blight-resistance gene in one of these extra chromosomes could account for the observed deviations.

TABLE IV

Resistant (F_1 × Susceptible) × Susceptible

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
556*a*(30) × *S. tuberosum*	767	58	10	5·8 : 1	< 7 : 1	$Ra_2(Ra_3)Rb_1$ × Recessive
556*b*(2) × *S. tuberosum*	683, 740	85	91	0·93 : 1	< 1 : 1	(Rb_3) (1) × Recessive
556*b*(4) × *S. tuberosum*	684, 741, 742	210	82	2·6 : 1	< 3 : 1	$(Ra_3)Rb_1$ (2) × Recessive

(1) Several of the A resistant seedlings were tested with the B strain. All were resistant.
(2) Several of the A resistant seedlings were tested with the B strain. Both resistants and susceptibles were present.

The results obtained in third backcrossed progenies are shown in Table V. All these families can be traced back to a common resistant ancestor, 556*b*(4), included in Table IV, which was credited with the Ra_3 gene in an unpaired chromosome and the Rb_1 gene in a paired chromosome. The results show that two of the three possible resistant genotypes obtainable from it are represented in Table V and that all have inherited the univalent bearing the Ra_3 gene. Tests made with the B strain of blight served to confirm the presence or absence of the Rb gene.

Owing to the low fertility of the F_1 hybrids, few F_2 seedlings were obtained. In a test involving 14 F_2 plants, 12 proved to be resistant and 2 susceptible. A ratio greater than 15 : 1 was expected. Three resistant F_2 seedlings

were, however, backcrossed to *S. tuberosum* and the segregations in the resulting progenies are set out in Table VI. Two of the three plants were found to contain both an Ra and an Rb gene, and the segregations indicate that one of these genes was present in an unpaired chromosome. By further backcrossing, as shown in Table VII, it was found that the Ra gene was located in a univalent and that the Rb gene was contained in a paired chromosome. In a cytological examination of the resistant parent 571(18), 60 chromosomes were counted in the root tips.

TABLE V

Resistant [(*F*$_1$ × *Susceptible*) × *Susceptible*] × *Susceptible*

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
684*a*(13) × *S. tuberosum*	770, 867, 868, 869	251	108	2·3 : 1	< 3 : 1	(Ra_3)Rb_1 (1) × Recessive
684*a*(49) × *S. tuberosum*	771, 772	47	69	0·68 : 1	< 1 : 1	(Ra_3) (2) × Recessive
742*b*(2) × *S. tuberosum*	958, 959, 960	190	289	0·65 : 1	< 1 : 1	(Ra_3) (3) × Recessive

(1) Several of the A resistant seedlings were tested with the B strain. Both resistants and susceptibles were present.
(2) Several of the A resistant seedlings were tested with the B strain. All were susceptible.
(3) 742*b*(2) was susceptible to the B strain.

TABLE VI

Resistant *F*$_2$ × *Susceptible*

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
568(18) × *S. tuberosum*	686, 687	242	142	1·7 : 1	< 3 : 1	(Ra_3)Rb_1 (1) × Recessive
571(18) × *S. tuberosum*	691, 692, 693, 768	266	136	1·9 : 1	< 3 : 1	(Ra_3)Rb_1 (1) × Recessive
571(31) × *S. tuberosum*	694	81	79	1 : 1	1 : 1	Rb_1 × Recessive

(1) Several of the A resistant seedlings were tested with the B strain. Both resistants and susceptibles were present.

Various progenies, which form a second backcrossed generation from the F_2, were raised and tested and the segregations are shown in Table VII. All the resistant parents were selected from progenies discussed in Table VI, in which the possible number of genotypes is limited to three. The only effective genes involved in Table VI are Ra_3 and Rb_1, therefore the resistant parents in Table VII may possess either or both. These three alternatives are sufficient to explain the segregations obtained, and the presence or absence of the Rb gene was confirmed by a number of tests with the B strain of blight.

Cytological examination of three of the parent seedlings revealed the presence of extra chromosomes. 50 chromosomes were counted in root-tip preparations of 691*a*(39) and 692*b*(12), and 51 in 691*a*(80).

A number of progenies, obtained by self- or cross-fertilising resistant plants, were tested and the results are shown in Table VIII. All the parents except one were found to possess only a single resistance gene which, according to the segregations, was most frequently located in an unpaired chromosome. With the exception of progeny 937 all are related to progenies discussed in previous tables.

TABLE VII

Resistant (F_2 × Susceptible) × Susceptible

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
686*a*(66) × *S. tuberosum*	943	34	25	1·4 : 1	< 3 : 1	$(Ra_3)Rb_1$ (1) × Recessive
687*b*(10) × *S. tuberosum*	948, 949	34	62	0·55 : 1	< 1 : 1	(Ra_3) × Recessive
687*b*(29) × *S. tuberosum*	950, 951, 1100	140	196	0·71 : 1	< 1 : 1	(Ra_3) (2) × Recessive
691*a*(39) × *S. tuberosum*	773	63	81	0·77 : 1	< 1 : 1	(Ra_3) (3) × Recessive
691*a*(80) × *S. tuberosum*	774, 775	122	117	1·0 : 1	< 1 : 1	(Ra_3) (3) × Recessive
692*a*(29) × *S. tuberosum*	776	60	120	0·5 : 1	< 1 : 1	(Ra_3) (3) × Recessive
692*a*(52) × *S. tuberosum*	870, 872, 873, 874	271	132	2·0 : 1	< 3 : 1	$(Ra_3)Rb_1$ (4) × Recessive
692*b*(12) × *S. tuberosum*	777, 778	147	71	2·0 : 1	< 3 : 1	$(Ra_3)Rb_1$ (4) × Recessive
693*a*(43) × *S. tuberosum*	779	86	30	2·86 : 1	< 3 : 1	$(Ra_3)Rb_1$ × Recessive
693*a*(44) × *S. tuberosum*	780, 782, 783, 784, 785	179	193	0·93 : 1	1 : 1	Rb_1 × Recessive
693*a*(59) × *S. tuberosum*	786, 787	89	80	1·1 : 1	1 : 1	Rb_1 × Recessive
693*a*(101) × *S. tuberosum*	877	129	130	1 : 1	1 : 1	Rb_1 (5) × Recessive

(1) 686*a*(66) was resistant to the B strain.
(2) 687*b*(29) was susceptible to the B strain.
(3) Several of the A resistant seedlings were tested with the B strain. All were susceptible.
(4) Several of the A resistant seedlings were tested with the B strain. Both resistants and susceptibles were present.
(5) Several of the A resistant seedlings were tested with the B strain. All were resistant.

TABLE VIII

Resistants Selfed or Crossed

Parentage	Ref. No.	No. of Seedlings R	No. of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
800(2) selfed	937	237	134	1·8 : 1	< 3 : 1	(Ra_3) (1)
687*b*(29) × 800(2)	1101	30	18	1·66 : 1	< 3 : 1	(Ra_3) (2) × (Ra_3)
692*a*(52) × 800(2)	875	65	20	3·25 : 1	< 7 : 1	(Ra_3)Rb_1 (3) × (Ra_3)
742*b*(2) × 800(2)	961	107	55	1·9 : 1	< 3 : 1	(Ra_3) (4) × (Ra_3)
740*c*(1) N.S.	965	65	48	1·35 : 1	< 3 : 1	(Rb_3) (5)
774*a*(10) N.S.	967	86	51	1·7 : 1	< 3 : 1	(Ra_3) (6)
775(29) N.S.	968	45	31	1·45 : 1	< 3 : 1	(Ra_3) (6)
778*a*(43) N.S.	969	152	56	2·7 : 1	< 3 : 1	Rb_1 (6)
778*a*(65) N.S.	970	34	18	1·9 : 1	< 3 : 1	(Ra_3) (6)

N.S. = Natural self.

(1) 800(2) was susceptible to the B strain.
(2) 687*b*(29) was susceptible to the B strain. Included also in Table VII.
(3) 692*a*(52) was resistant to the B strain. Included also in Table VII.
(4) 742*b*(2) was susceptible to the B strain. Included also in Table V.
(5) 740*c*(1) was resistant to the B strain. Derived from progeny 740 in Table IV.
(6) Derived from progenies 774, 775, and 778 respectively in Table VII.

DISCUSSION

The evidence for believing that potatoes are allopolyploid in constitution and that their basic chromosome number is 6, is now sufficiently well established to warrant its use in interpreting the results of genetical experiments. It is likely that interspecific hybridity has played a large part in the formation of the known potato species. This view is further supported by cytological evidence of secondary association in several species and by the presence of two satellite-carrying chromosomes in the somatic cells of *S. tuberosum*. Also Choudhuri (1943) has observed in 24-chromosome species irregularities of chromosome behaviour which are usually seen only in hybrids.

The evidence of tetraploid inheritance put forward by Lunden (1937) is not inconsistent with this view. Similar modes of inheritance have been observed by Lawrence (1929, 1931) in the allo-octoploid *Dahlia variabilis* in which several flower colour genes are inherited as if the nucleus is tetrasomic. The inheritance of the red and blue pigments in *S. tuberosum* suggest a parallel to the behaviour of the two pigment groups, orange and magenta, which are combined in *D. variabilis*. Lunden required seven factors to explain colour inheritance in *S. tuberosum*, three of which were directly concerned with the production of red and one with the production of blue pigment in the tubers. It seems probable that the red and blue pigments of *S. tuberosum* originated in different species and were later brought together by species hybridisation in much the same manner as were the two pigments in *D. variabilis*.

Similarly, in the experiments on inheritance of resistance to wart disease (*Synchytrium endobioticum*) Lunden found that three factors were necessary to explain his results, viz. one independent and two complementary factors. Here again a separate origin of these two kinds of factors may be visualised.

In the present investigations the two genes Ra and Rb controlling resistance to blight in *S. demissum* are presumed to have arisen in this manner. Their independent functioning and the difference in the degree of resistance which they confer all suggest a separate origin.

The self-fertilising and intercrossing of plants resistant only to the A strain of blight gave progenies wholly susceptible to the B strain. No increase in resistance was therefore apparent as a result of increasing the dosage

of the Ra gene. On the other hand an increase of resistance may have occurred with an increased gene dosage, but insufficient in extent to reach the level necessary to counteract the virulence of the B strain. If such a quantitative relationship does not exist, adequate scope is provided for the genetical treatment of other physiological forms of the fungus which may arise. The reactions of the two strains of blight employed do not provide conclusive evidence on this question, but indications of different degrees of susceptibility were noted in several progenies infected with the B strain.

In the hybrid, Ref. No. 735, bred from *S. Rybinii* × *S. demissum*, both allosyndetic and autosyndetic pairing presumably occurred, and a certain amount of affinity therefore existed between the chromosomes which bear the Ra_2 and Ra_3 genes. These chromosomes, in the absence of their normal partners, apparently pair, but since the cross was difficult to effect and only one hybrid seed was obtained the degree of affinity cannot be great. A similar affinity exists between the chromosomes carrying Rb_2 and Rb_3. The hybrids of *S. demissum* and *S. tuberosum* (Ref. No. 429) contained 12 unpaired chromosomes, and the results show that the Ra_3 and Rb_3 genes were carried in them. It follows therefore that the Ra and Rb genes have arisen from phylogenetically different sources, but that the origins of the various Ra genes or the various Rb genes are related.

The highly resistant self-fertile plant, Ref. No. 735, bred from *S. Rybinii* ($n=12$) and *S. demissum* ($n=36$), resembled neither parent closely in outward appearance, but was more akin to the pollen parent *S. demissum*. Although it had 48 somatic chromosomes as in *S. tuberosum* very few triple hybrids were obtained, but subsequent backcrossing to *S. tuberosum* gave progenies which were normally prolific. A feature of these progenies was the high degree of pollen fertility attained. Most of the plants produced natural berries and some of the progenies consisted entirely of self-fertile individuals.

This fertility in conjunction with resistance to blight is a useful asset in the breeding of commercial varieties of potatoes. This type of work has been greatly handicapped by the lack of viable pollen, nearly all the best varieties being practically male sterile. The same difficulties arise in seedlings bred directly from *S. demissum* and *S. tuberosum*. It has been shown that these seedlings have an unbalanced chromosome complement and that genes controlling blight resistance are frequently located in a univalent chromosome which is liable to be lost. Few of the offspring are normally self-fertile, and seedlings selected for breeding purposes generally have to be fertilised with pollen taken from such of the commercial varieties as may be available.

An important line of development in potato breeding for commercially suitable varieties is the combination of resistance to blight along with field immunity from viruses A and X. The number of such field-immune varieties is small, and the commercially popular ones at present available are unhappily self-sterile. In these circumstances progress can best be accelerated when blight resistance and pollen fertility are conjoined in plants whose chromosome behaviour is normal and regular. These conditions are fulfilled in the triple hybrids mentioned above and thus render practicable the combining of blight resistance with field immunity.

In breeding the triple hybrid plants the species *S. Rybinii* acted primarily as a genetical "bridge" by which the heritable characters of the more important species, *S. demissum* and *S. tuberosum*, were united in cytologically successful units. In view of the heteroploid series which forms the genus *Solanum* and of the self- and cross-incompatibility encountered within it, the use of "bridging" species for effecting interspecific hybridisation should prove highly advantageous in future work.

Summary

1. *Phytophthora infestans* consists of a basic or common form of wide distribution, together with a number of more or less isolated biotypes which have developed from it. All forms are stable under normal conditions.

2. The reaction of potatoes to the attacks of the disease is genetically controlled and is unaffected by the age of the plant.

3. Two strains of blight were used in these experiments: A, the common strain, and B, a more virulent strain developed from it.

Segregations of resistant and susceptible plants following infection with the two strains have been traced through several generations of hybrids bred from

(a) *S. Rybinii*, *S. demissum*, and *S. tuberosum*.

(b) *S. demissum* and *S. tuberosum*.

4. In so far as the two strains of blight are concerned, it is suggested that the inheritance of resistance to them is controlled by two factors of different phylogenetic origin, designated Ra and Rb. The former confers resistance to the A strain of blight and the latter to both strains. A concentration of Ra genes did not confer resistance to the B strain of blight.

5. The results obtained are in harmony with published cytological evidence indicating that the species of potato concerned are of hybrid origin with 6 as the most probable basic chromosome number. Accordingly the inheritance of resistance to blight is explained on the basis of the allopolyploid character of the species, *S. Rybinii* being treated as an allotetraploid, *S. tuberosum* as an allo-octoploid, and *S. demissum* as an allododecaploid.

For assistance in the cytological work thanks are due to Dr H. C. Choudhuri and Mr J. M. Main.

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XX.—Inheritance of Resistance to Blight (*Phytophthora infestans*) in Potatoes: Unbalanced Segregations.

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Introduction

Studies of the inheritance of resistance to two strains, A and B, of the blight fungus (*Phytophthora infestans*) in derivatives of the triple hybrid (*S. Rybinii* × *S. demissum*) × *S. tuberosum* and in hybrids descended from *S. demissum* × *S. tuberosum* led to the conclusion that resistance was controlled by two genes, designated Ra and Rb, of different phylogenetic origin, the former conferring resistance against strain A and the latter against both strain A and strain B (Black, 1943).

In continuation of these studies a number of progenies bred from selections in the first backcross generation of the aforementioned triple hybrids have been examined for their reaction to the common or A strain of blight. The family tree (fig. 1) illustrates the source

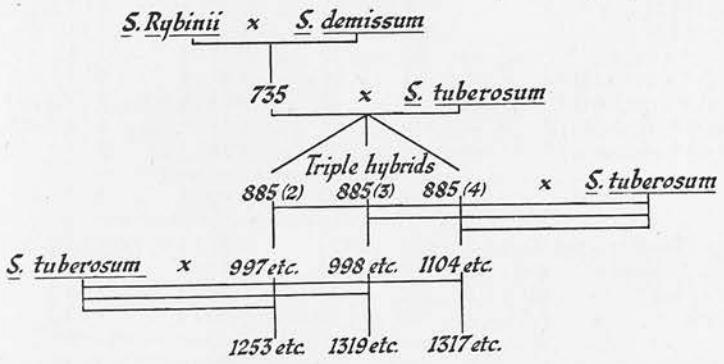

Fig. 1.

of the various generations and shows in general form the ancestry of the seedlings to be discussed in section (*a*).

The triple hybrids used in this extended work were three sister seedlings, 885(2), 885(3), and 885(4). From self- and backcross-progenies, tested for their reaction to blight strains A and B, it was found (Black, 1943) that the probable genotypic constitutions of these seedlings were:—

885(2)	RaRb.
885(3)	RaRbRb.
885(4)	RaRbRb.

Although only the common or A strain of *P. infestans* was employed in making the routine progeny tests throughout the work to be described, plants used as parents were separately

TABLE I

Ref. No.	Parentage	A Strain No. of Seedlings R	A Strain No. of Seedlings r	Theoretical Ratio	B Strain No. of Seedlings R	B Strain No. of Seedlings r	Theoretical Ratio	Suggested Genotypes (Dominant Genes only)
735	*S. Rybinii* × *S. demissum*	1	0	∞ : 0	1	0	∞ : 0	Recessive * × $Ra_2Ra_2Ra_3Ra_3Rb_1Rb_1Rb_3Rb_3$
897	735 selfed	71	0	∞ : 0	63	1	15 : 1	$Ra_2Ra_3Rb_1Rb_3$
994	735 × *S. Rybinii*	16	0	∞ : 0	14	2	3 : 1	$Ra_2Ra_3Rb_1Rb_3$ × Recessive *
884–6	735 × *S. tuberosum*	7	0	∞ : 0	5	2	3 : 1	$Ra_2Ra_3Rb_1Rb_3$ × Recessive †
995	884(1) × *S. tuberosum*	21	6	3 : 1	12	15	1 : 1	Ra_xRb_1 × Recessive †
996	885(1) × do.	94	99	1 : 1	0	73	0 : ∞	Ra_x × Recessive †
997	885(2) × do.	216	75	3 : 1	125	124	1 : 1	Ra_xRb_3 × Recessive †
998	885(3) × do.	114	19	7 : 1	121	44	3 : 1	$Ra_xRb_1Rb_3$ × Recessive †
1112	885(3) selfed	75	0	63 : 1	54	4	15 : 1	$Ra_xRb_1Rb_3$
1104	885(4) × *S. tuberosum*	103	25	7 : 1	78	33	3 : 1	$Ra_xRb_1Rb_3$ × Recessive †
1015	885(4) selfed	288	7	63 : 1	31	0	15 : 1	$Ra_xRb_1Rb_3$
999	886(2) × *S. tuberosum*	39	36	1 : 1	0	52	0 : ∞	Ra_x × Recessive †
1016	886(2) selfed	42	16	3 : 1	0	18	0 : ∞	Ra_x
1116	1015*a*(1) selfed	..	..	..	58	0	∞ : 0	$Ra_xRa_xRb_1Rb_1Rb_3Rb_3$?

The female parent is named first throughout.

* The full recessive genotype of *S. Rybinii* is $ra_1ra_1rb_1rb_1$.

† The full recessive genotype of *S. tuberosum* is $ra_1ra_1ra_2ra_2rb_1rb_1rb_2rb_2$.

TABLE II.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1286	997*a*(5) * N.S.	87	31	2·81 : 1	3 : 1	Ra
1287	997*a*(25) * N.S.	84	23	3·65 : 1	3 : 1	Ra
1288	997*a*(30) * N.S.	105	75	1·40 : 1	3 : 1	Ra
1289	997*a*(44) † N.S.	95	48	1·98 : 1	3 : 1	Rb
1290	997*a*(51) † N.S.	168	73	2·30 : 1	3 : 1	Rb
1331	997*d*(16) † N.S.	200	88	2·27 : 1	3 : 1	Rb
1277	997*a*(4) * × 997*a*(5) *	62	30	2·07 : 1	3 : 1	Ra × Ra
1278	997*a*(5) * × 997*a*(25) *	71	52	1·37 : 1	3 : 1	Ra × Ra
1279	997*a*(5) * × 997*a*(61) *	78	48	1·63 : 1	3 : 1	Ra × Ra
1280	997*a*(25) * × 997*a*(61) *	142	66	2·15 : 1	3 : 1	Ra × Ra
1281	997*a*(30) * × 997*a*(61) *	67	38	1·76 : 1	3 : 1	Ra × Ra
		1159	572	2·03 : 1	3 : 1	
1253	Craigs Defiance × 997*a*(44) †	148	171	0·87 : 1	1 : 1	Recessive × Rb
1263	Golden Wonder × do.	90	108	0·83 : 1	1 : 1	
1267	Kerr's Pink × do.	80	85	0·94 : 1	1 : 1	
1268	Majestic × do.	18	28	0·64 : 1	1 : 1	
		336	392	0·86 : 1	1 : 1	
1254	Craigs Defiance × 997*a*(51) †	282	289	0·98 : 1	1 : 1	Recessive × Rb
1257	Di Vernon × do.	113	125	0·90 : 1	1 : 1	
1258	Epicure × do.	251	266	0·94 : 1	1 : 1	
1264	Golden Wonder × do.	65	104	0·63 : 1	1 : 1	
1266	Katahdin × do.	59	65	0·91 : 1	1 : 1	
1269	Majestic × do.	64	64	1·00 : 1	1 : 1	
1270	Manxman × do.	201	258	0·78 : 1	1 : 1	
1271	Ninetyfold × do.	158	176	0·90 : 1	1 : 1	
1275	Southesk × do.	206	222	0·93 : 1	1 : 1	
		1399	1569	0·89 : 1	1 : 1	

* = Immune from A strain. Susceptible to B strain.

† = Immune from both A and B strains.

N.S. = Natural Self.

examined for their reactions to both the A and B strains. The results of these independent tests are indicated by * and † signs in the tables. The suggested parental genotypes are thus based on parental reaction to both the A and B strains of the fungus and on the type of segregation shown in the progeny tests.

Additional data on blight inheritance have been obtained from multiple hybrid material which originated at the hands of the late Dr Wilson of St Andrews. As far back as 1908

TABLE III.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1299	998*a*(7) † N.S.	64	28	2·29 : 1	3 : 1	Rb
1300	998*a*(18) † N.S.	36	14	2·57 : 1	3 : 1	Rb
1301	998*a*(43) † N.S.	109	38	2·87 : 1	3 : 1	Rb
1302	998*c*(10) † N.S.	194	68	2·85 : 1	3 : 1	Rb
		403	148	2·72 : 1	3 : 1	
1303	998*c*(13) † N.S.	109	12	9·08 : 1	15 : 1	RaRb or RbRb
1304	998*c*(20) † N.S.	165	15	11·00 : 1	15 : 1	RaRb or RbRb
		274	27	10·15 : 1	15 : 1	
1319	Craigs Defiance × 998*a*(7) †	96	75	1·28 : 1	1 : 1	Recessive × Rb
1322	Ninetyfold × do.	68	81	0·84 : 1	1 : 1	
		164	156	1·05 : 1	1 : 1	
1323	833*a*(25) *998*a*(7) †	111	43	2·58 : 1	3 : 1	Ra × Rb
1324	834*b*(6) * × do.	265	84	3·15 : 1	3 : 1	
1325	835*a*(4) * × do.	80	32	2·50 : 1	3 : 1	
		456	159	2·87 : 1	3 : 1	
1256	Craigs Defiance × 998*a*(18) †	281	313	0·90 : 1	1 : 1	Recessive × Rb
1265	Golden Wonder × do.	99	98	1·01 : 1	1 : 1	
1276	Southesk × do.	327	361	0·91 : 1	1 : 1	
		707	772	0·92 : 1	1 : 1	
1327	E.P.C.106 × 998*a*(43) †	70	103	0·68 : 1	1 : 1	Recessive × Rb
1328	E.P.C.210 × do.	56	62	0·90 : 1	1 : 1	
		126	165	0·76 : 1	1 : 1	

* = Immune from A strain. Susceptible to B strain.
† = Immune from both A and B strains.
N.S. = Natural Self.

833*a*(25), 834*b*(6), and 835*a*(4) were selected from progenies 833–5 quoted in Table V.
E.P.C. 106 and E.P.C. 210 are varieties of *S. andigenum*.

Dr Wilson was engaged in interspecific hybridisation of potatoes. Among the seedlings which were the outcome of his work was one W.800(2) derived as the 5th generation hybrid from a series of interspecific crosses involving five different species of potato. The family tree of W.800(2) was previously published (Robb, 1921) and it is here reproduced in fig. 2, with two corrections in classification.

When Dr Wilson was engaged in these interspecific hybridisations little was known regarding the systematics of the tuber-bearing Solanums and few species had been described. On the authority of Dr R. N. Salaman, privately communicated, the plants which Dr Wilson

described as *S. tuberosum* (Mexican sp.) and *S. etuberosum* were in reality *S. demissum* and *S. edinense* respectively. Thus the five species involved in the breeding of W.800(2) were *S. commersonii*, *S. maglia*, *S. edinense*, *S. demissum*, and *S. tuberosum*.

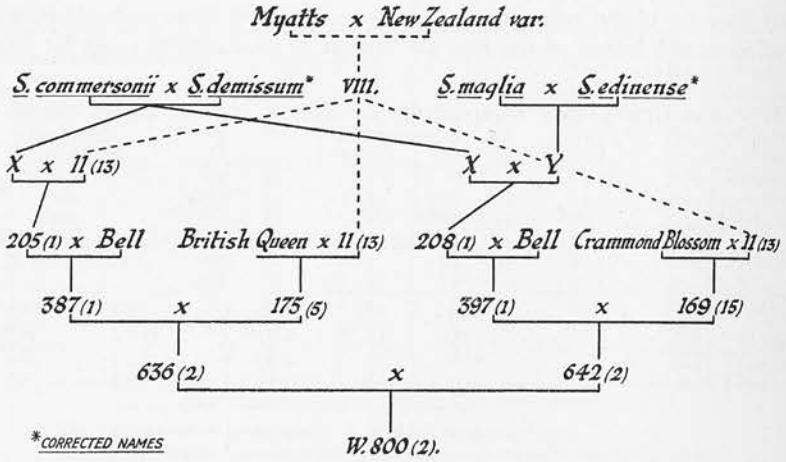

FIG. 2.

W.800(2) is a highly self-fertile seedling which is immune from the A strain of blight but is susceptible to the B strain. This seedling has been used by the writer directly as a parent in a number of hybridisations and has served as the source of blight resistance in an extensive breeding programme which has now reached the 8th generation from the original interspecific crosses by which resistance was introduced. The actual variety of *S. demissum* used by Dr Wilson cannot now be ascertained, but the available evidence indicates that it was the same as that employed by the writer in the hybridisations discussed earlier and from which the progenies described in section (*a*) are descended.

No critical cytological examination of the material has been attempted, but chromosome counts of representatives of the parent plants included in Tables II–VIII showed that in neither root tip nor pollen-mother-cell preparations was there any deviation from 48 somatic or 24 gametic chromosome complements.

EXPERIMENTAL RESULTS

(*a*) *Triple Hybrid Derivatives*

The original cross and the results from testing the early generations of the triple hybrid (*S. Rybinii* × *S. demissum*) × *S. tuberosum* and their derivatives have already been given (Black, 1943). For the purpose of linking up the current data with those already published, the segregations given in the earlier generations are reproduced in Table I. All the progenies included in Tables II–IV were derived from seedlings selected from progenies of which either one or both parents are referred to in Table I.

Table II shows the segregations obtained by selfing, intercrossing, and backcrossing resistant seedlings selected in the 1st backcross generation of the triple hybrid 885(2). Selfing and intercrossing resulted in segregations which, with one exception, showed an excess of recessives over the expected 3 : 1 ratio. The segregations varied rather widely, but the mean ratio was 2·03 immunes to 1 susceptible. "A" resisters and "B" resisters gave comparable results. Two of the "B" resistant seedlings 997*a*(44) and 997*a*(51) were used as pollen parents in backcrossing to *S. tuberosum* varieties. A 1 : 1 ratio was expected, but all gave an excess of recessives except one family which segregated in equal proportions. These progenies, on the whole, were reasonably consistent in their deviation from the expected ration.

Table III contains the second generation derivatives of triple hybrid 885(3). All the

plants selected as parents from family 998 were immune from both A and B strains of blight, but the progenies were tested with the A strain only. Four selfed progenies, Ref. Nos. 1299, 1300, 1301, and 1302, deviated fairly consistently in favour of recessives from the 3 : 1 ratio. Two progenies, Ref. Nos. 1303 and 1304, whose parents must be either RaRb or RbRb in constitution, deviated in similar fashion from the expected 15 : 1 ratio. The resistant seedlings selected as pollen parents for backcrossing, viz. 998*a*(7), 998*a*(18), and 998*a*(43), all proved to be simplex and although the results obtained are slightly variable they show, as a whole, a definite excess of susceptible offspring. The female parents of progenies 1323, 1324, and 1325 are "A" resistant seedlings selected from families 833–5 (Table V) which are discussed in the next section. As the results show, however, they do not affect the general trend of the deviations in the segregations.

Table IV shows the segregations of the second generation derivatives of triple hybrid 885(4). All the resistant selections used as parents in this group were immune from both

TABLE IV.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1306	1104*a*(3) † N.S.	134	12	11·17 : 1	15 : 1	RaRb or RbRb
1332	1104*a*(6) † N.S.	190	20	9·50 : 1	15 : 1	RaRb or RbRb
		324	32	10·13 : 1	15 : 1	
1307	1104*a*(16) † N.S.	124	44	2·82 : 1	3 : 1	Rb
1308	1104*a*(23) † N.S.	23	8	2·88 : 1	3 : 1	Rb
		147	52	2·83 : 1	3 : 1	
1317	Epicure × 1104*b*(19) †	151	253	0·60 : 1	1 : 1	Recessive × Rb
1320	Craigs Defiance × 1104*b*(19) †	38	58	0·66 : 1	1 : 1	
		189	311	0·61 : 1	1 : 1	

N.S. = Natural Self.
† = Immune from both A and B strains.

the A and B strains of blight. Two of them, 1104*a*(3) and 1104*a*(6), gave ratios indicating the presence of two factors either RaRb or RbRb while the remainder were simplex in constitution. The deviations from each of the three segregation ratios expected are consistent with those already discussed in Tables II and III.

(*b*) *Multiple Species Hybrid Derivatives*

The progenies discussed in this section were derived from the 5th generation seedling W.800(2). Since the first five generations were bred and raised by the late Dr Wilson at St Andrews, the writer has no information regarding their reaction to infection with blight. Seedling W.800(2), however, proved to be immune from the A strain but susceptible to B. Although it possessed several undesirable characters it was fortunately self-fertile.

The segregation obtained by selfing W.800(2) (Table V) shows a significant deviation from the expected 3 : 1 ratio in favour of recessives. Likewise an excess of susceptible plants resulted from the crossing of W.800(2) with cultivated varieties where a 1 : 1 ratio was expected.

A seedling W.967*c*(38), bred from W.800(2) and Bishop, was used extensively as female parent in crosses with various susceptible varieties and seedlings. The results of the progeny tests (Table VI) again show a definite excess of recessives. These segregations indicate

that W.800(2) and its backcross seedling W.967*c*(38) are similarly constituted in respect of the blight-resistance character. It is worthy of note that the segregations obtained were similar although W.800(2) was employed as male parent and W.967*c*(38) as female parent in their respective hybridisations. Accordingly reciprocal crosses can be assumed to behave in similar fashion.

Table VII contains a series of progenies representing the third backcrossed generation from W.800(2). In all cases a 1 : 1 ratio was expected. All but 6 progenies show an excess

TABLE V.—1ST-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
937	W.800(2) B.S.	237	134	1·77 : 1	3 : 1	Ra
833–5	Craigs Defiance × W.800(2)	500	637	0·78 : 1	1 : 1	Recessive × Ra
837	Epicure × do.	79	132	0·60 : 1	1 : 1	
1076	Great Scot × do.	73	143	0·51 : 1	1 : 1	
1077	Imperia × do.	182	255	0·71 : 1	1 : 1	
1079	Ninetyfold × do.	68	78	0·87 : 1	1 : 1	
		902	1245	0·72 : 1	1 : 1	

B.S. = Bagged Self.
W.800(2) is immune from A strain but susceptible to B strain.

TABLE VI.—2ND-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
652	W.967*c*(38) × Flourball	29	44	0·66 : 1	1 : 1	Ra × Recessive
653	do. × Katahdin	207	269	0·77 : 1	1 : 1	
655	do. × 70(13)	54	67	0·81 : 1	1 : 1	
759	do. × The Alness	153	176	0·87 : 1	1 : 1	
760	do. × Liddesdale Lad	50	60	0·83 : 1	1 1	
761	do. × Pepo	60	92	0·65 : 1	1 : 1	
763	do. × Shamrock	57	54	1·06 : 1	1 : 1	
764	do. × 121(2)	199	225	0·88 : 1	1 : 1	
855	do. × M.233(13)	45	44	1·02 : 1	1 : 1	
1095	do. × T(*a*)	71	88	0·81 : 1	1 : 1	
		925	1119	0·83 : 1	1 : 1	

W.967*c*(38) is immune from A strain but susceptible to B strain.

of recessives and the mean deviation in favour of recessives is smaller than was obtained in the progenies bred directly from W.800(2) and W.967*c*(38).

Segregations resulting from the selfing of one 1st- and five 2nd-generation seedlings derived from W.800(2) are set out in Table VIII. The proportions of immunes and susceptibles are somewhat variable, ranging from 2·00 : 1 to 3·76 : 1, but the mean deviation shows a comparatively small though definite excess of recessives compared with the expected 3 : 1.

TABLE VII.—3RD-GENERATION DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
839	594(86) × Liddesdale Lad	55	59	0·93 : 1	1 : 1	Ra × Recessive
1081	651(10) × M.233(13)	51	65	0·78 : 1	1 : 1	do.
1082	do. × T(*a*)	132	144	0·92 : 1	1 : 1	do.
844	653*a*(115) × Gladstone	53	36	1·47 : 1	1 : 1	do.
845	do. × Liddesdale Lad	65	76	0·86 : 1	1 : 1	do.
847	do. × Pepo	60	42	1·43 : 1	1 : 1	do.
850	653*a*(140) × The Alness	39	45	0·87 : 1	1 : 1	do.
919	653*b*(103) × do.	76	76	1·00 : 1	1 : 1	do.
923	do. × Edgecote Purple	36	52	0·69 : 1	1 : 1	do.
924	do. × Kepplestone Kidney	112	105	1·07 : 1	1 : 1	do.
925	do. × Pepo	92	86	1·07 : 1	1 : 1	do.
1092	653*e*(22) × T(*a*)	78	85	0·92 : 1	1 : 1	do.
927–8	653*e*(25) × The Alness	63	69	0·91 : 1	1 : 1	do.
930	do. × Pepo	40	51	0·78 : 1	1 : 1	do.
931	655(34) × The Alness	68	90	0·76 : 1	1 : 1	do.
934	655(39) × Suttons Early Regent	168	197	0·85 : 1	1 : 1	do.
1093	759*b*(5) × Cardinal	58	59	0·98 : 1	1 : 1	do.
		1246	1337	0·93 : 1	1 : 1	

TABLE VIII.—SELFED DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
856	594(10) N.S.	128	34	3·76 : 1	3 : 1	Ra
1096	762(1) N.S.	143	48	2·98 : 1	3 : 1	Ra
936	764*a*(15) N.S.	144	45	3·20 : 1	3 : 1	Ra
1329	834*b*(6) N.S.	93	37	2·51 : 1	3 : 1	Ra
1098	850*a*(24) N.S.	116	58	2·00 : 1	3 : 1	Ra
1099	855(14) N.S.	136	50	2·72 : 1	3 : 1	Ra
		760	272	2·79 : 1	3 : 1	

N.S. = Natural Self.

DISCUSSION

The various progenies described in Tables II–VIII are, with a few exceptions, consistent in showing an excess of recessives. Though the extent of the deviations from normal ratios are variable they suggest by their unidirectional variance that influences other than pure chance have been in operation. In order to compare the average deviations of the various groups of progenies the totals have been brought together in Table IX and tested for goodness of fit. It will be seen that some of the segregations show a reasonably good approximation to simple Mendelian ratios while in other cases the probability is extremely small.

All the progenies derived from the triple hybrids (Tables II, III, IV) are further condensed in Table X, and those from the multiple hybrid W.800(2) (Tables V, VI, VII, VIII) in Table XI. Although the triple hybrids inherited their resistance from *S. demissum* alone while W.800(2) had two sources, *S. demissum* and *S. edinense*, these two groups of seedlings show a close similarity in their corresponding segregations.

TABLE IX.—TOTALS OF GROUPS IN TABLES II–VIII

Table	Expected		Observed		No. of Seedlings			$\chi 2$	Deviation	
	R	r	R	r	R	r	Total		D.F.	P
II	1	1	0·86	1	336	392	728	4·30	1	0·05–0·02
	1	1	0·89	1	1399	1569	2968	9·74	1	Small
	3	1	2·03	1	1159	572	1731	59·74	1	Very small
III	1	1	1·05	1	164	156	320	0·20	1	0·70–0·50
	1	1	0·92	1	707	772	1479	2·86	1	0·10–0·05
	1	1	0·76	1	126	165	291	5·23	1	0·05–0·02
	3	1	2·72	1	403	148	551	1·02	1	0·50–0·30
	3	1	2·87	1	456	159	615	0·24	1	0·70–0·50
	15	1	10·15	1	274	27	301	3·81	1	0·10–0·05
IV	1	1	0·61	1	189	311	500	29·77	1	Very small
	3	1	2·83	1	147	52	199	0·14	1	0·80–0·70
	15	1	10·13	1	324	32	356	4·56	1	0·05–0·02
V	1	1	0·72	1	902	1245	2147	54·80	1	Very small
	3	1	1·77	1	237	134	371	24·46	1	Very small
VI	1	1	0·83	1	925	1119	2044	18·41	1	Very small
VII	1	1	0·93	1	1246	1337	2583	3·21	1	0·10–0·05
VIII	3	1	2·79	1	760	272	1032	1·01	1	0·50–0·30

TABLE X.—TOTALS DERIVED FROM TRIPLE HYBRIDS (TABLES II, III, IV)

Expected		Observed		No. of Seedlings			χ^2	Deviation	
R	r	R	r	R	r	Total		D.F.	P.
1	1	0·87	1	2921	3365	6286	31·36	1	Very small
3	1	2·32	1	2165	931	3096	42·46	1	Very Small
15	1	10·14	1	598	59	657	8·36	1	Small

TABLE XI.—TOTALS DERIVED FROM MULTIPLE HYBRID (TABLES V, VI, VII, VIII)

Expected		Observed		No. of Seedlings			χ^2	Deviation	
R	r	R	r	R	r	Total		D.F.	P.
1	1	0·83	1	3073	3701	6774	58·22	1	Very small
3	1	2·46	1	997	406	1403	11·60	1	Small

Table XII contains the combined data of Table X–XI. Analysis of these grand totals shows that the segregations as a whole do not agree with standard theoretical ratios. Unbalanced segregations of this type may be ascribed to double reduction where a high degree of homology exists between corresponding sets of chromosomes as in the case of autotetraploids. Cadman (1942) in dealing with the reactions of cultivated potatoes to virus X found a reasonably consistent excess of recessives and concluded that the potato was probably autotetraploid in constitution. In the present case, however, similar excesses cannot be explained on the same basis for the plants concerned are indubitably complex hybrids and, consequently, cannot be strictly autopolyploids. Nevertheless homologies between chromosomes derived from the different species used may exist and consequently multivalent formations with double reduction may account for some of the excess of recessives which are such a marked feature of the observed segregations.

There is, however, too large an excess of recessives for this explanation to be fully acceptable. It seems probable that the unbalanced segregations are largely due to the frequency of fusion of the different kinds of gametes. Apparently some degree of incompatibility exists between *S. demissum* on the one hand and *S. Rybinii* and *S. tuberosum* on the other, since hybridisations of these species are comparatively unprolific. Table XIII shows the average number of seeds per berry obtained from such hybrid and backcross matings. The fact that prolificacy increases after backcrossing to *S. tuberosum* indicates that factors

contributing towards partial incompatibility are being eliminated, just as many of the "wild" characters introduced by *S. demissum* are being eliminated and replaced by the more desirable characters of cultivated varieties. Thus it is suggested that gametes possessing genes for blight resistance are at some disadvantage compared with their recessive competitors. Such differential affinity would result in the production of more susceptible

TABLE XII.—COMBINED TOTALS (TABLES II–VIII)

Expected	Observed	No. of Seedlings			χ^2	Deviation	
R r	R r	R	r	Total		D.F.	P.
1 : 1	0·85 : 1	5994	7066	13060	87·99	1	Very Small
3 : 1	2·36 : 1	3162	1337	4499	53·40	1	Very small
15 : 1	10·14 : 1	598	59	657	8·36	1	Small
				18216			

TABLE XIII.—FERTILITY IN HYBRID AND BACKCROSSED PROGENIES

Cross	No. of Berries	No. of Seeds	Average No. of Seeds per Berry	Highest No. of Seeds per Berry
S. tuberosum × *S. demissum*	0	0	0·0	0
S. demissum × *S. tuberosum*	7	98	14·0	36
F_1 (*S. demissum* × *S. tuberosum*) × *S. tuberosum*	35	1172	33·5	70
2nd Backcross to *S. tuberosum*	23	1887	82·0	118
3rd Backcross to *S. tuberosum*	12	1673	139·4	210
S. demissum × *S. Rybinii*	0	0	0·0	0
S. Rybinii × *S. demissum*	1	1	1·0	1
F_1 (*S. Rybinii* × *S. demissum*) × *S. tuberosum*	8	12	1·5	3
Triple hybrid × *S. tuberosum*	20	1930	96·5	214
2nd Backcross to *S. tuberosum*	14	3447	246·2	377

seedlings than would be expected under conditions of complete compatibility. The excess would not be constant but would vary according to the genetical constitutions of the particular plants employed as parents.

On that basis it might be expected that the deviation in favour of recessives would tend to decrease with continued backcrossing to the cultivated type. Some indication that such takes place is apparent in the backcross ratios of three consecutive generations contained in Tables V, VI, and VII respectively. The ratios are 0·72 : 1 (Table V), 0·83 : 1 (Table VI), and 0·93 : 1 (Table VII). The last-mentioned ratio refers to distribution in the 8th generation from the wild ancestor, *S. demissum*, and consequently segregations even more closely approaching normal might be expected in later generations. But it is probable that strictly normal ratios may never be attained since blight-resistance is essentially a *demissum* character, and so long as it is retained so also may be some residual incompatibility to upset the balance of segregations.

The evidence for regarding differential compatibility of gametes as an explanation of the unbalanced segregations is supported by the widely different powers of seed production which potatoes exhibit together with the complete self- and cross-incompatibility so frequently encountered among species. Seed production varies between wide limits; the highest number recorded by the writer is 777 in one berry and the lowest 0, while most of the intermediate numbers may be found. In addition, most berries and particularly those from hybrid plants, contain a proportion of rudimentary seeds indicating that although fusion of gametes had failed, the stimulus was present. References to incompatibility in potatoes are numerous and some embody a wide range of results, *e.g.* Bukasov (1937) and Choudhuri (1944). In a study of the genetics of incompatibility Pushkarnath (1942) established 8

intra-sterile but interfertile groups of potatoes each possessing a different pair of 5 sterility factors which, operating in various combinations, controlled self- and cross-incompatibility.

Resistance to blight, being physiological in nature, must be based upon and react with a general nexus of physiological conditions within the plant. Any alteration in these mutual relationships must alter the potency of any one, as, for example, resistance to a fungous disease. Müller (1941) declared that resistance genes do not produce an "all or none" reaction but function only as accelerators of the defence reaction of which both susceptible and resistant genotypes are capable. Müller and Börger (1941) were able to increase resistance in a plant by introducing into its tissues an inoculum derived from a strain to which it was resistant. Later treatment with a strain to which it was susceptible resulted in abnormally small lesions. The first inoculation upset the normal balance, accelerating the defence reaction before the second inoculation was made and a certain amount of apparent resistance was induced. That susceptibles as well as resistants have a defence reaction can be accepted since it is well known that cultivated varieties vary considerably in the degree of susceptibility and the extent of the damage suffered. Among resistant plants differences in degree of resistance are also established by the reactions to the various strains of blight.

The manifestation of resistance must therefore be effected by a physiological complex which in the genetical sense is controlled by a number of factors. In view of the facts that:—

(1) susceptibles, selfed or intercrossed, gave only susceptibles;
(2) "A" resisters, selfed or intercrossed, failed to produce "B" resisters; and
(3) segregation ratios were indicative of simple Mendelian ratios;

it may be assumed that resistance is controlled by major genes, *e.g.* Ra and Rb. It is upon these two genes at least that the primary reactions, immunity, or susceptibility depend. Minor genes which merely control the degree of susceptibility in susceptible varieties and act as unidentifiable modifiers in resistants may also be assumed.

Reddick and Mills (1938) were able to increase the virulence of blight on certain resistant plants by manipulation and culture of the fungus. Moreover, this increased level of virulence was found to be maintained for at least 20 generations (Reddick, 1943). This induced change of virulence was, in effect, the creation of a new strain against which the plant had no inherent defence. Presumably the type of plant employed was representative of a low level of resistance.

The fact that such new physiological strains of a fungus can and do appear under field conditions is of extreme importance because blight resistant varieties, when introduced into commerce, may serve as steps in building up virulence. If virulent strains can be built up in this way to such an extent as to overcome the maximum resistance available in the gene population of potatoes, then the production of blight-proof varieties will be impossible. In this connection Reddick (1943) is of the opinion that the commercialisation of intermediate types of resistants, *i.e.* seedlings immune only from the weaker strains of blight, should be prohibited, and that tests should be made with a built-up strain of the parasite several steps more virulent than the strain commonly found in the field. By eliminating these intermediate types of resistants it should be found possible to develop a class of plants which would be immune under all field conditions at present envisaged. This point of view, however, presupposes a quantitative rather than a qualitative difference in the virulence of strains which has not so far been confirmed. It would, therefore, be advantageous to ascertain if the fungus can increase in virulence to such an extent and, if so, whether it must pass through the intermediate steps for full development.

Summary

1. The reactions of two groups of seedlings, (*a*) triple-hybrid derivatives, and (*b*) multiple-species hybrid-derivatives, to infection with the common or "A" strain of blight are recorded.

2. The available evidence indicates that resistance to blight is controlled by major genes upon which depend the major reaction, resistance, or susceptibility, and by minor genes which determine the degree of susceptibility in susceptible varieties and act as unidentifiable modifiers in resistants.

3. Segregation of resistant and susceptible plants in the progenies show a highly consistent excess of recessive individuals compared with the standard 1 : 1, 3 : 1, and 15 : 1 ratios.

4. It is suggested that the excess of recessives may be due in part to chromosome homologies leading to multivalent formation and double reduction. In the material under discussion, however, the excess is largely due to the differential compatibility of gametes arising from residual incompatibility factors associated with the original "wild" material.

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XX.—Inheritance of Resistance to Blight (*Phytophthora infestans*) in Potatoes: Comparison of A and B Strains.*

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Introduction

Previous reports (Black, 1943, 1945) on the resistance of potatoes to the blight fungus (*Phytophthora infestans*) have shown the existence of at least two major genetic factors (Ra and Rb) in the host, and the occurrence of not less than two strains (A and B) of the pathogen.

From the studies then reported, it was concluded that the two genes had been brought into the potato from different phyletic sources and that one, Ra, when in the dominant state, conferred resistance to strain A, while similarly Rb conferred resistance to strain B.

Also, it was concluded that a series of modifying or minor genes in the crop plant bore on the general situation produced by the major genes, and that these determined the degree of susceptibility in susceptible phenotypes and the power to withstand the fungus in resistant ones.

Throughout the experiments, the progenies obtained showed consistently segregations of resistant from susceptible plants not in conformity with the usual 1 : 1, 3 : 1 and 15 : 1 Mendelian ratios. The excess of recessives then obtained might be due, in part, to the occurrence of chromosome homologies leading to multivalent formation and double reduction. Alternatively, however, it appeared that incompatibility factors derived from the wild species employed in the breeding work had a selective influence on the union of gametes, and hence on the distribution of resistants and susceptibles in the progenies.

In the experiments all progenies were tested by inoculation with the common or A strain of the fungus, except in the case of certain early generations (Black, 1945, Table I), where both the A and the B strains were employed. The studies reported here continue and extend the investigations, and are devoted to a comparison of strains A and B based on results obtained from progeny testing with the B strain.

Since most of the B-resistant parent plants employed in the experiments were derived from the three triple hybrids 885(2), 885(3) and 885(4) previously described (Black, 1945), their family tree is here reproduced and extended (fig. 1) to illustrate the origin of the progenies which provided the experimental material referred to here. Most of this material is comparable with that previously employed in the A strain tests, and the genes involved may be traced through the various generations.

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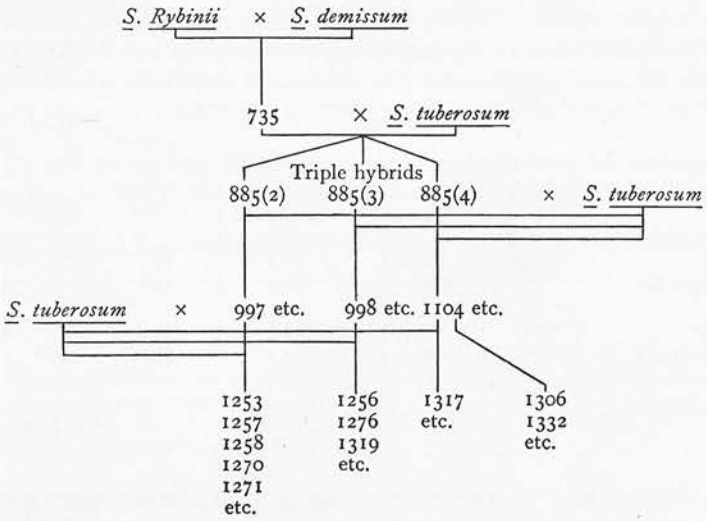

FIG. 1.

EXPERIMENTAL RESULTS

In Table I are shown the segregations obtained in 2nd-generation derivatives of 885(2) tested with strain B. The resistant parent seedlings 997*a*(44) and 997*a*(51) on selfing both

TABLE I.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1289	997*a*(44) N.S.	142	53	2·68 : 1	3 : 1	Rb
1435	Gladstone × 997*a*(44)	67	109	0·61 : 1	1 : 1	Recessive × Rb
1620	997*a*(51) N.S.	265	96	2·76 : 1	3 : 1	Rb
1258	Epicure × 997*a*(51)	89	87	1·02 : 1	1 : 1	Recessive × Rb
1491	791*a*(116) × 997*a*(51)	98	125	0·78 : 1	1 : 1	
		187	212	0·88 : 1	1 : 1	

N.S. = Natural Self.

gave approximations to the 3 : 1 ratio and on back-crossing to susceptible varieties approximations to the 1 : 1 ratio. An excess of recessives was observed in four of the five cases. Similar progenies were previously tested with strain A (Black, 1945, Table II), and the segregations then observed are compared in Table II with the segregations resulting from the B test. It will be seen that both strains give similar segregations, the progenies apparently consisting of B resistants and recessives only. Thus the single gene Rb controls resistance to both the A and B strains.

The families shown in Table III represent the 3rd-generation derivatives of triple hybrid 885(2). One of the parent plants of each progeny was selected from families 1253, 1257, 1258, 1270 and 1271 previously tested with strain A (Black, 1945, Table II), where a single gene Rb was believed to be in operation. This belief receives confirmation from the data obtained from B strain tests and presented here in Table III. These results show a consistent

TABLE II.—COMPARISON OF SEGREGATIONS IN STRAIN A AND STRAIN B TESTS

Parentage	A Strain			B Strain		
	Seedlings tested	Ratio		Seedlings tested	Ratio	
		Observed	Theoretical		Observed	Theoretical
997*a*(44) Selfed	143	1·98 : 1	3 : 1	195	2·68 : 1	3 : 1
Susceptible × 997*a*(44)	728	0·86 : 1	1 : 1	176	0·61 : 1	1 : 1
997*a*(51) Selfed	241	2·30 : 1	3 : 1	361	2·76 : 1	3 : 1
Susceptible × 997*a*(51)	2968	0·89 : 1	1 : 1	399	0·88 : 1	1 : 1

TABLE III.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(2) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings		Ratio		Suggested Genotypes (Dominant Genes only)
		R	r	Observed	Theoretical	
1679–80	1253*a*(12) × 834*c*(29)*	153	141	1·09 : 1	1 : 1	Rb × Ra
1595	1253*a*(15) × Katahdin	33	24	1·37 : 1	1 : 1	Rb × Recessive
1596	do. × Dr McIntosh	74	59	1·25 : 1	1 : 1	
1684	do. × 834*b*(6)*	48	54	0·89 : 1	1 : 1	Rb × Ra
		155	137	1·13 : 1	1 : 1	
1585	Southesk × 1257*a*(7)	104	97	1·07 : 1	1 : 1	Recessive × Rb
1524	1258*a*(19) × 910*a*(123)	74	80	0·93 : 1	1 : 1	Rb × Recessive
1605	do. × Pepo	69	85	0·81 : 1	1 : 1	
		143	165	0·87 : 1	1 : 1	
G908	1270*a*(5) × Shamrock	41	57	0·72 : 1	1 : 1	Rb × Recessive
G907	do. (11) × do.	49	41	1·19 : 1	1 : 1	
G909	do. (15) × do.	41	57	0·72 : 1	1 : 1	
G910	do. (16) × do.	62	55	1·13 : 1	1 : 1	
		193	210	0·92 : 1	1 : 1	
1688	1270*b*(9) × 910*a*(123)	104	108	0·96 : 1	1 : 1	Rb × Recessive
1687	do. × 834*c*(29)*	276	281	0·98 : 1	1 : 1	Rb × Ra
		380	389	0·97 : 1	1 : 1	
1692	1271*b*(9) × 834*c*(29)*	51	78	0·65 : 1	1 : 1	Rb × Ra
1681	1253*a*(12) × 1306*a*(2)†	292	114	2·56 : 1	3 : 1	Rb × RaRb
1598	do. (15) × do.	249	70	3·56 : 1	3 : 1	
1689	1270*b*(9) × do.	245	88	2·78 : 1	3 : 1	
1693	1271*b*(9) × do.	87	31	2·81 : 1	3 : 1	
1685	1253*a*(15) × 1332*a*(6)†	275	119	2·31 : 1	3 : 1	Rb × Rb
		1148	422	2·72 : 1	3 : 1	

* = Immune from A strain but susceptible to B strain (Black, 1945, Table V).
† = Immune from both A and B strains (see Table X).

excess of recessives, with the exception of those referring to the progenies derived from 1253*a*(15), where the ratios show a wider variation. It will be noted that the segregations obtained from Rb × Ra genotypes are similar to those resulting from Rb × Recessive. Such results would be expected in these tests, since the Ra gene contributes no apparent resistance to the B strain of the fungus.

In Table IV are shown the results of testing 2nd-generation derivatives of triple hybrid 885(3) with strain B. The segregations indicate that the resistant seedlings 998*a*(7) and

TABLE IV.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
(1299) (1525)	998*a*(7) N.S.	215	56	3·84 : 1	3 : 1	Rb
1493	791*a*(116) × 998*a*(7)	45	57	0·79 : 1	1 : 1	Recessive × Rb
1324	834*b*(6)* × do.	85	63	1·35 : 1	1 : 1	Ra × Rb
		130	120	1·08 : 1	1 : 1	
1622	998*a*(18) N.S.	190	67	2·84 : 1	3 : 1	Rb
1494	791*a*(116) × 998*a*(18)	72	103	0·70 : 1	1 : 1	Recessive × Rb
1499	831(113) × do.	59	69	0·86 : 1	1 : 1	
		131	172	0·76 : 1	1 : 1	

* = Immune from A strain but susceptible to B strain (Black, 1945, Table V).
N.S. = Natural Self.

998*a*(18) possess only the gene Rb in their constitution. Progenies derived from these seedlings were previously tested with strain A (Black, 1945, Table III) and similar segregations were obtained. The results are compared in Table V. The Rb gene accordingly controls resistance to both A and B strains in this material.

TABLE V.—COMPARISON OF SEGREGATIONS IN STRAIN A AND STRAIN B TESTS

Parentage	A Strain			B Strain		
	Seedlings tested	Ratio Observed	Ratio Theoretical	Seedlings tested	Ratio Observed	Ratio Theoretical
998*a*(7) Selfed	92	2·29 : 1	3 : 1	271	3·84 : 1	3 : 1
Susceptible × 998*a*(7)	320	1·05 : 1	1 : 1	250	1·08 : 1	1 : 1
998*a*(18) Selfed	50	2·57 : 1	3 : 1	257	2·84 : 1	3 : 1
Susceptible × 998*a*(18)	1479	0·92 : 1	1 : 1	303	0·76 : 1	1 : 1

Table VI contains the segregations observed in 3rd-generation derivatives of triple hybrid 885(3) tested with strain B. The resistant parent plants were selected from progenies 1256 and 1276 which were previously tested with strain A (Black, 1945, Table III). The presence of the gene Rb in these resistant selections is confirmed by the B strain test. Again this material shows, on the average, an excess of recessive segregates.

Table VII contains the segregations observed in 2nd-generation derivatives of triple hybrid 885(4) tested in season 1946 with strain B. The parent seedlings concerned, 1104*a*(3) and 1104*c*(2) on the basis of these segregations, apparently possessed two Rb genes. A

TABLE VI.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(3) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1600*ab*	1256*a*(23) × Katahdin	119	130	0·91 : 1	1 : 1	Rb × Recessive
1601	do. × 910*a*(123)	32	39	0·82 : 1	1 : 1	
		151	169	0·89 : 1	1 : 1	
G911*a*	1276*a*(1) × Shamrock	26	48	0·54 : 1	1 : 1	Rb × Recessive
G912*b*	do. (4) × do.	73	84	0·87 : 1	1 : 1	
G886*a*	do. (12) × do.	49	49	1·0 : 1	1 : 1	
1441	1276*b*(6) × 910*a*(123)	69	56	1·23 : 1	1 : 1	
G889	1276*b*(10) × Shamrock	42	43	0·98 : 1	1 : 1	
		259	280	0·93 : 1	1 : 1	

TABLE VII.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN B IN 1946

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1528*c*	1104*a*(3) N.S.	208	15	13·87 : 1	15 : 1	RbRb
1488*ab*	Craigs Defiance × 1104*a*(3)	343	132	2·60 : 1	3 : 1	Recessive × RbRb
1496*a*	791*a*(116) × do.	142	62	2·29 : 1	3 : 1	
		485	194	2·50 : 1	3 : 1	
1503*ab*	835*a*(4)* × 1104*a*(3)	322	139	2·32 : 1	3 : 1	Ra × RbRb
1518*abc*	882(5)† × 1104*a*(3)	502	80	6·28 : 1	7 : 1	RaRb × RbRb
1489	Craigs Defiance × 1104*c*(2)	158	49	3·22 : 1	3 : 1	Recessive × RbRb
1497*a*	791*a*(116) × do.	145	58	2·50 : 1	3 : 1	
		303	107	2·83 : 1	3 : 1	
1505*ab*	835*a*(4)* × 1104*c*(2)	339	196	1·73 : 1	3 : 1	Ra × RbRb
1521*ab*	882(5)† × 1104*c*(2)	469	77	6·09 : 1	7 : 1	RaRb × RbRb

* = Immune from A strain but susceptible to B strain (Black, 1945, Table V).
† = Immune from both A and B strains (see Table XI).
N.S. = Natural Self.

progeny derived from 1104*a*(3) selfed was previously tested with strain A (Black, 1945, Table IV) and was found to have two resistance genes, but under A test only it was impossible to decide whether the constitution was RaRb or RbRb. On the 1946 evidence contained in Table VII the latter appeared to be correct.

In 1947 and 1948, however, results (Table VIII) were obtained differing in character from those observed in 1946. These segregations indicate that only a single Rb gene was in operation, and suggest either the mutation of the other Rb gene or a change in virulence of the fungus. If a mutation affecting one Rb gene had occurred between the seasons 1946 and 1947, then seed secured in 1945 would have given the same results irrespective of whether

TABLE VIII.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN B IN 1947 AND 1948

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1528*b*	1104*a*(3) N.S.	228	65	3·51 : 1	3 : 1	R?Rb
1563*ab*	Craigs Defiance × 1104*a*(3)	280	246	1·14 : 1	1 : 1	Recessive × R?Rb
1567*a*	Epicure × do.	131	120	1·09 : 1	1 : 1	
1583*ab*	Southesk × do.	332	329	1·01 : 1	1 : 1	
1591*a*	791*a*(116) × do.	132	97	1·36 : 1	1 : 1	
1496*b*	do. × do.	82	67	1·22 : 1	1 : 1	
		957	859	1·11 : 1	1 : 1	
1504*ac*	835*a*(4)* × 1104*a*(3)	305	288	1·06 : 1	1 : 1	Ra × R?Rb
1518*d*	882(5)† × 1104*a*(3)	116	37	3·14 : 1	3 : 1	RaRb × R?Rb
1624*a*	1104*c*(2) N.S.	156	59	2·64 : 1	3 : 1	R?Rb
1564*ab*	Craigs Defiance × 1104*c*(2)	276	301	0·92 : 1	1 : 1	Recessive × R?Rb
1572*a*	Gladstone × do.	188	184	1·02 : 1	1 : 1	
1584*ab*	Southesk × do.	340	384	0·89 : 1	1 : 1	
		804	869	0·93 : 1	1 : 1	
1506*a*	835*a*(4)* × 1104*c*(2)	47	38	1·24 : 1	1 : 1	Ra × R?Rb
1589*abc*	655(43)* × do.	99	82	1·21 : 1	1 : 1	
		146	120	1·22 : 1	1 : 1	
1521*c*	882(5)† × 1104*c*(2)	194	66	2·94 : 1	3 : 1	RaRb × R?Rb
1522*a*	do. × do.	162	70	2·31 : 1	3 : 1	
		356	136	2·62 : 1	3 : 1	

* = Immune from A strain but susceptible to B strain (Black, 1945, Tables V and VI).
† = Immune from both A and B strains (see Table XI).
N.S. = Natural Self.

TABLE IX.—COMPARISON OF SEGREGATIONS IN TESTS WITH STRAIN B IN 1946 AND 1947–48

Parentage	Strain B 1946 Seedlings tested	Strain B 1946 Ratio Observed	Strain B 1946 Ratio Theoretical	Strain B 1947–48 Seedlings tested	Strain B 1947–48 Ratio Observed	Strain B 1947–48 Ratio Theoretical
1104*a*(3) Selfed .	223	13·87 : 1	15 : 1	293	3·51 : 1	3 : 1
Recessive × 1104*a*(3)	679	2·50 : 1	3 : 1	1816	1·11 : 1	1 : 1
Ra × do.	461	2·32 : 1	3 : 1	593	1·06 : 1	1 : 1
RaRb × do.	582	6·28 : 1	7 : 1	153	3·14 : 1	3 : 1
1104*c*(2) Selfed .	..	..	15 : 1	215	2·64 : 1	3 : 1
Recessive × 1104*c*(2)	410	2·83 : 1	3 : 1	1673	0·93 : 1	1 : 1
Ra × do.	535	1·73 : 1	3 : 1	266	1·21 : 1	1 : 1
RaRb × do.	546	6·09 : 1	7 : 1	492	2·62 : 1	3 : 1

it was sown in 1946, 1947 or 1948. This was not so. The seed of all the material in Tables VII and VIII with a reference number below 1529 was secured in 1945, yet the two tables show results widely different in character. It is concluded, therefore, that the B strain of the fungus had increased in virulence between the end of routine tests in 1946 and the beginning of the 1947 season. In all the material tested the only gene affected was one carried by 1104*a*(3) and 1104*c*(2), and consequently it must confer a degree of resistance higher than the effective level of the 1946 B strain yet lower than that of the altered strain in its 1947 and 1948 condition. This gene is not identical with Ra or Rb and is designated R?. Presumably the increase in virulence was comparatively small, since it failed to affect the segregations in progenies derived from all other sources. The results of the 1946 tests are compared with those of 1947–48 in Table IX.

In Table X are shown the segregations obtained with strain B in progenies representing the 3rd-generation derivatives of triple hybrid 885(4). Seedling 1306*a*(2) was selected from

TABLE X.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1630	1306*a*(2) N.S.	147	54	2·72 : 1	3 : 1	RaRb
1565	Craigs Defiance × 1306*a*(2)	54	65	0·83 : 1	1 : 1	
1569	Epicure × do.	144	162	0·89 : 1	1 : 1	
1573	Gladstone × do.	159	160	0·99 : 1	1 : 1	
1576	Kerr's Pink × do.	32	80	0·40 : 1	1 : 1	
1580	Majestic × do.	42	67	0·63 : 1	1 : 1	
1582	Ninetyfold × do.	35	38	0·92 : 1	1 : 1	Recessive × RaRb
1592	791*a*(116) × do.	234	262	0·89 : 1	1 : 1	
1594	831(113) × do.	130	174	0·75 : 1	1 : 1	
1654	do. × do.	86	102	0·84 : 1	1 : 1	
1610	1–106 × do.	116	106	1·09 : 1	1 : 1	
1611	2–349 × do.	111	109	1·02 : 1	1 : 1	
		1143	1325	0·86 : 1	1 : 1	
1590	655(43)* × 1306*a*(2)	129	163	0·79 : 1	1 : 1	
1656–7	835*a*(4)* × do.	91	80	1·14 : 1	1 : 1	Ra × RaRb
1613	Falke* × do.	87	115	0·76 : 1	1 : 1	
1618	Robusta* × do.	96	96	1·00 : 1	1 : 1	
		403	454	0·89 : 1	1 : 1	
1681	1253*a*(12)† × 1306*a*(2)	292	114	2·56 : 1	3 : 1	
1598	1253*a*(15)† × do.	249	70	3·56 : 1	3 : 1	Rb × RaRb
1689	1270*b*(9)† × do.	245	88	2·78 : 1	3 : 1	
1693	1271*b*(9)† × do.	87	31	2·81 : 1	3 : 1	
		873	303	2·88 : 1	3 : 1	
1728	1332*a*(6) N.S.	115	48	2·40 : 1	3 : 1	Rb
1685	1253*a*(15)† × 1332*a*(6)	275	119	2·31 : 1	3 : 1	Rb × Rb

* = Immune from A strain but susceptible to B strain.
† = Immune from both A and B strains (see Table III).
N.S. = Natural Self.

a selfed progeny of 1104*a*(3) which has been discussed in Tables VII, VIII and IX. The results show that 1306*a*(2) carries the Rb gene which was unaffected by the change in virulence of the fungus. In addition an Ra gene is also present, as shown by the results of the double test (strain A followed by strain B) set out in Table XII. Possibly this gene is the same as the one which conferred resistance to the 1946 B strain but failed against the greater

virulence of the 1947–48 form. Unfortunately confirmation is lacking because seed of 1306*a*(2) did not become available until 1947.

The segregations obtained in progenies derived from 1332*a*(6) are similar to those of 1306*a*(2). Since 1332*a*(6) was bred from 1104*a*(6) (Black, 1945, Table IV) and no check tests on similar material were made with the A strain, it is impossible to decide whether the Ra gene is present in 1332*a*(6). In relation to the B strain, however, its effective constitution is Rb.

The progenies bred from 1306*a*(2) and 1332*a*(6) each show an excess of recessives, although the extent of the deviations from the numbers expected vary considerably in different cases.

Table XI refers to the segregations in progenies bred from hybrid 882(5). This seedling is not related to the triple hybrid material and their derivatives but is descended from progeny 692 (Black, 1943, Table VI), and its origin is illustrated in fig. 2.

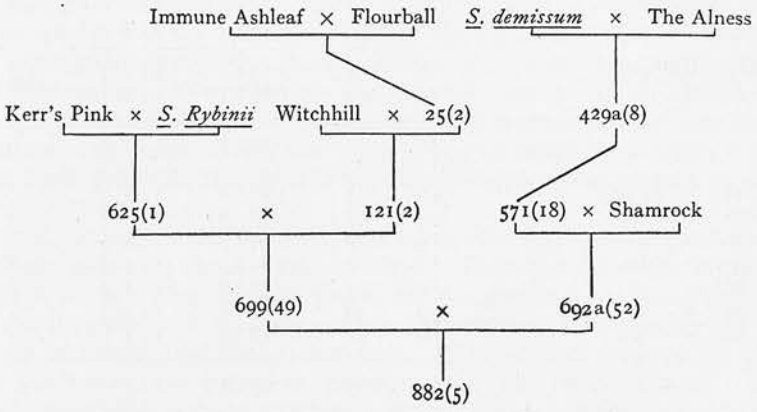

FIG. 2.

In crosses with recessive types and with the A resistant seedling 834*c*(29) it shows a close approximation to the 1 : 1 ratio, deviating only slightly towards an excess of recessives. With a sister A-resistant seedling 834*b*(6), however, a deviation in favour of the dominant type is pronounced. The numbers of seedlings tested are too small to be conclusive, but it may be significant that 834*b*(6) progenies contain a small excess of dominants under A strain test (Table XIII). The results of the double test (Table XII) show that 882(5) possesses an Ra gene in addition to Rb.

In order to confirm the presence or absence of the Ra gene in parent seedlings, certain progenies were tested first with strain A and the survivors with strain B. The results are shown in Table XII. The first group of progenies contained no plants resistant to A and susceptible to B, but all segregated into B resisters and recessives in the proportion of approximately 1 : 1, therefore the gene involved in each case is Rb.

The second group, in which 882(5), 1104*a*(3), 1104*c*(2) and 1306*a*(2) were crossed with recessives, contained a proportion of A resistant–B susceptible forms in addition to recessives and B resisters. Two different genes must therefore be in operation, and the segregations obtained indicate that the constitution of the resistant parents is RaRb (or R?Rb in the case of 1104*a*(3) and 1104*c*(2)).

The third group, bred from 882(5), 1104*a*(3) and 1104*c*(2) crossed with A resistant–B susceptible types, was expected to segregate in the proportion of 7 : 1 under A test and 1 : 1 under B test. The observed ratios fit closely in respect of the 1 : 1 ratio but less so in the case of the 7 : 1.

The last group, obtained by intercrossing and selfing RaRb (or R?Rb) genotypes, should, under normal circumstances, segregate in the proportion of 15 : 1 under A test and 3 : 1 under B test. Again the excess of recessives is greater in the higher ratio.

TABLE XI.—DERIVATIVES OF HYBRID 882(5) TESTED WITH STRAIN B

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Suggested Genotypes (Dominant Genes only)
1508	882(5) × Katahdin	136	127	1·07 : 1	1 : 1	RaRb × Recessive
1509	do. × do.	113	129	0·88 : 1	1 : 1	
1510	do. × Dr McIntosh	69	78	0·88 : 1	1 : 1	
1511	do. × M233(13)	69	84	0·82 : 1	1 : 1	
1516	do. × 910*a*(123)	265	258	1·03 : 1	1 : 1	
1517	do. × do.	105	122	0·86 : 1	1 : 1	
1669	do. × do.	55	58	0·95 : 1	1 : 1	
1670	do. × do.	74	56	1·32 : 1	1 : 1	
		886	912	0·97 : 1	1 : 1	
1662	882(5) × 834*b*(6)*	29	19	1·53 : 1	1 : 1	RaRb × Ra
1663	do. × do.	68	42	1·62 : 1	1 : 1	
		97	61	1·59 : 1	1 : 1	
1512	882(5) × 834*c*(29)*	360	355	1·01 : 1	1 : 1	RaRb × Ra
1513	do. × do.	219	238	0·92 : 1	1 : 1	
1514	do. × do.	109	129	0·84 : 1	1 : 1	
1515	do. × do.	72	86	0·84 : 1	1 : 1	
1665	do. × do.	20	23	0·87 : 1	1 : 1	
1666	do. × do.	35	46	0·76 : 1	1 : 1	
1667	do. × do.	92	78	1·18 : 1	1 : 1	
		907	955	0·95 : 1	1 : 1	

* = Immune from A strain but susceptible to B strain (Black, 1945, Table V).

TABLE XII.—PROGENIES TESTED WITH STRAINS A AND B CONSECUTIVELY

Ref. No.	Parentage	Number of Seedlings Killed by A	Killed by B	Survived	Ratio (R : r) A Test	B Test	Suggested Genotypes (Dominant Genes only)
1600*b*	1256*a*(23) × Katahdin	50	..	44	0·88 : 1	0·88 : 1	Rb × Recessive
1585*ab*	Southesk × 1257*a*(7)	97	..	104	1·07 : 1	1·07 : 1	Recessive × Rb
1445*c*	Craigs Defiance × 1335*a*(5)†	62	..	69	1·11 : 1	1·11 : 1	Recessive × Rb
1446*b*	Majestic × do.	43	..	47	1·09 : 1	1·09 : 1	
		252	..	264	1·05 : 1	1·05 : 1	
1508*b*, 1509*ab*	882(5) × Katahdin	98	92	179	2·77 : 1	0·94 : 1	RaRb × Recessive
1563*b*	Craigs Defiance × 1104*a*(3)	99	40	145	1·87 : 1	1·04 : 1	Recessive × R?Rb
1564*b*	do. × 1104*c*(2)	94	56	126	2·0 : 1	0·84 : 1	Recessive × R?Rb
1569*bc*	Epicure × 1306*a*(2)	35	19	52	2·03 : 1	0·96 : 1	Recessive × RaRb
1592*cd*	791*a*(116) × do.	64	40	120	2·50 : 1	1·15 : 1	
		390	247	622	2·23 : 1	0·98 : 1	
1513*c*, 1515	882(5) × 834*c*(29)*	40	73	102	4·37 : 1	0·90 : 1	RaRb × Ra
1504*c*	835*a*(4)* × 1104*a*(3)	53	62	106	3·17 : 1	0·92 : 1	Ra × R?Rb
1589*bc*	655(43)* × 1104*c*(2)	22	35	73	4·91 : 1	1·28 : 1	Ra × R?Rb
		115	170	281	3·92 : 1	0·99 : 1	
1522*a*	882(5) × 1104*c*(2)	31	39	162	6·48 : 1	2·31 : 1	RaRb × R?Rb
1630*bc*	1306*a*(2) N.S.	29	25	147	5·93 : 1	2·72 : 1	RaRb
		60	64	309	6·22 : 1	2·49 : 1	

* = Immune from A strain but susceptible to B strain.
† = *S. demissum* derivative immune from both A and B strains.
N.S. = Natural Self.

Discussion

It is frequently found that segregation ratios of resistant to susceptible seedlings in progenies bred from *S. demissum* hybrids may bear little resemblance to standard Mendelian ratios. This is particularly noticeable in the earlier generations derived from *S. demissum* and *S. tuberosum*. The peculiar figures obtained appear to be due partly to the complexity of chromosome homologies often found in such interspecific hybrids, and partly to the unbalanced chromosome complements arising from the mating of plants with different chromosome numbers. The difficulties associated with irregular numbers of chromosomes may be avoided by synthesising, in the first place, a blight-resistant hybrid with 48 chromosomes such as seedling 735. This plant, bred from *S. Rybinii* ($2n=24$) × *S. demissum* ($2n=72$), has 48 chromosomes, as have also the triple hybrids obtained by crossing it with *S. tuberosum*. In an examination of this material, Thomas (1945) found that chromosome differentiation between these species was not sufficient to affect pairing to any extent. Lehmann (1941), in genetical experiments involving different varieties of *S. demissum*, found that inheritance was disomic in character. No doubt the chromosome relationships in species hybrids may be less simple, and autosyndesis, allosyndesis, and even random pairing may occur. Under these circumstances, the mode of inheritance in breeding for resistance to blight is best regarded as disomic in basis although, through different chromosome homologies, it may not be consistently so.

The segregations set out in the foregoing tables are very similar to those obtained in the series of tests involving the A strain of blight. Thus, the behaviour of the Rb gene in relation to the B strain is identical with that of the Ra gene in relation to the A strain. The presence of the Ra gene in B resistant varieties is ineffective in increasing the resistance to the B strain or in altering the segregation ratio. A variety carrying the Rb gene alone, if crossed with a recessive, will segregate only B resistant and recessive types. In such cases the A strain is as efficient for test purposes as the B strain. If both Ra and Rb genes are present, however, the progeny will consist of recessives, A resisters and B resisters. The A strain will identify the recessive segregates, while the B strain, if applied to the survivors, will attack the A resisters, leaving only the B resisters alive. In such progenies inoculation with the B strain alone will eliminate the recessives and the A resisters without differentiation.

The deviations from standard Mendelian ratios observed in segregations resulting from tests with the B strain are comparable with those previously obtained in the A strain tests (Black, 1945). In the latter material the consistent excess of recessives was attributed mainly to differential compatibility of gametes, whereby the more frequent association of residual incompatibility factors with typical *S. demissum* characters placed at a disadvantage those gametes carrying genes for blight resistance. If this is true for the Ra gene, it is equally true for the Rb. It was found that deviations tended to decrease with repeated backcrossing to cultivated varieties, due presumably to the progressive elimination of incompatibility factors. Further evidence of the approach to normal segregation ratios resulting from backcrossing in A-resistant material is shown in Table XIII. The progenies represent the 6th, 7th and 8th generations from the wild ancestor, *S. demissum*, and the number of seedlings involved is relatively large. Seedling W.800(2) (Black, 1945, Table V), crossed with a recessive, gave resistants and susceptibles in the proportion of 0·72 : 1 respectively. The seedlings selected from these progenies and used as parents, viz. 834*c*(29), W.967*c*(38), 833*a*(25), 835*a*(4) and 834*b*(6), all gave progenies showing a smaller deviation from the 1 : 1 ratio. Likewise, seedlings selected as parents from the cross W.967*c*(38) × Recessive, viz. 653*c*(35), 764*c*(11) and 655(43), gave segregations more closely approaching 1 : 1 than the families from which they were selected. The differences which these ratios exhibit presumably reflect the relative extent of incompatibility still persisting in the parental forms.

The instability of the blight fungus under changing environmental conditions has been observed by various investigators, *e.g.* Reddick and Mills (1938). In the present experiments an increase in the infective power of strain B has come to light by the unexpected change in segregation ratios explained in Tables VII, VIII and IX. The increase in virulence appears to be relatively small since no other progenies were affected, but it was sufficient to render ineffective a gene which previously conferred adequate resistance on the plants

TABLE XIII.—DERIVATIVES OF MULTIPLE HYBRID W.800(2) TESTED WITH STRAIN A

Generation	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio
1st	Recessive × W.800(2)*	902	1245	0·72 : 1
2nd	do. × 834*c*(29)	863	1101	0·78 : 1
2nd	W.967*c*(38) × Recessive†	925	1119	0·83 : 1
2nd	Recessive × 833*a*(25)	161	173	0·93 : 1
2nd	835*a*(4) × Recessive	740	798	0·93 : 1
2nd	Recessive × 834*b*(6)	433	405	1·07 : 1
2nd	W.967*c*(38) × Recessive†	925	1119	0·83 : 1
3rd	653*c*(35) × do.	295	344	0·86 : 1
3rd	764*c*(11) × do.	87	98	0·89 : 1
3rd	655(43) × do.	399	440	0·91 : 1

* Black, 1945, Table V.
† Black, 1945, Table VI.

possessing it. The precise cause of this altered virulence is not clear. It may have arisen by mutation during tests of that material at the end of the season 1946 or during subsequent culture in potato tubers for winter storage. It is customary to maintain and multiply specialised races of the fungus on the varieties on which they originally appeared and to which they were specially adapted. During routine tests, however, inoculum was sometimes prepared from the affected plants of the preceding test, and it is conceivable that in this way a mutant strain became isolated and was subsequently multiplied.

Since the Ra gene appears to provide no protection against attack by the B strain, it is unlikely that existing commercial varieties would suffer greater damage by strain B than is usually inflicted by the common strain. No doubt the predominant race of an organism exposed to natural selection is that which flourishes and multiplies best under the existing environmental conditions. Unless a mutant form can multiply as rapidly as the common race its survival will be prejudiced. It seems that the B strain, on the evidence of the infrequency of its appearance in the field, can make headway only in the environment provided by varieties resistant to the A strain, where it is protected from competition. Specialisation in parasitic fungi, therefore, need not imply additional danger to crops which are ordinarily susceptible, and in the ordinary course of events most mutant forms are probably shortlived. Such a low survival value in the face of competition would account for the failure to find new strains of blight in a survey of the disease in potato crops in Scotland (Black and Haigh, 1947).

SUMMARY

1. The reactions of seedling potato progenies of triple hybrid origin to infection with the B strain of blight are recorded and compared with segregations in related progenies previously tested with the A strain.

2. The evidence indicates that two independent major genes, Ra and Rb, confer resistance to strain A and to strains A and B respectively.

3. The segregations observed in derivatives of Ra material tested with strain A, and in derivatives of Rb material tested with either strain A or strain B, are similar in character. Compared with standard 1 : 1 and 3 : 1 ratios, they show a consistent excess of recessive segregates, due probably to the selective influence of incompatibility factors on the union of gametes.

4. An unexpected increase in the infective power of the B strain was revealed by a change in the character of segregations in one breeding line. A particular gene which conferred resistance to the original B strain was ineffective against the more virulent form, and the segregation ratios changed accordingly.

X.—Inheritance of Resistance to Blight (*Phytophthora infestans*) in Potatoes: Strain C and its Relationships.*

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Synopsis

The common strain A of the blight fungus (*Phytophthora infestans*) and two new strains, B and C, have been employed in testing potato varieties and seedling progenies, bred from the wild species *S. demissum*, for resistance to the disease. The reactions of seedlings to infection with strain C are compared with those of strains A and B. The C strain is shown to be more virulent than A, since it attacks some A resistant as well as all A susceptible plants. Likewise the B strain is more virulent than A. The difference between the pathogenicity of strains B and C, however, is not one of degree of virulence; one plant may be B resistant–C susceptible, while another may be B susceptible–C resistant. This difference is essentially of a qualitative nature. Resistance to these strains, which is manifested by the hypersensitive condition of the plant's cells, is produced in the presence of three major independent genes, Rc, Rb and Rbc, which confer resistance to strains A and C, A and B, and A, B and C respectively. Segregations in each case are similar in type, and are characterised by an excess of recessive individuals.

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Introduction

The common strain A of the blight fungus (*Phytophthora infestans*) and two new strains, B and C, have been employed for several years in testing potato varieties and seedling progenies for resistance to the disease. It has been shown in reports of earlier experiments involving strains A and B only (Black, 1943, 1945, 1949), that resistance in the host is controlled by at least two major genetic factors, Ra and Rb. When present in the dominant state, the gene Ra confers resistance to strain A, while the gene Rb confers resistance to both strains A and B. The phenotypic expression of these genes is believed to be subject to modification by a

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series of minor genes, which have the effect of differentiating degrees of resistance in the presence of major genes and degrees of susceptibility in the absence of such genes.

In these experiments, the proportions of resistant and susceptible segregates observed in the progenies were consistently unbalanced in favour of recessives by comparison with the usual 1 : 1, 3 : 1 and 15 : 1 Mendelian ratios. The excess of recessives may have been due, in part, to the occurrence of chromosome homologies leading to multivalent forma-

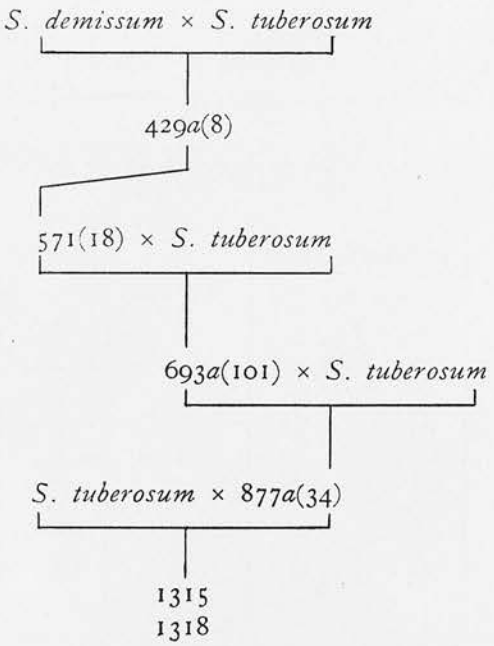

FIG. 1

tion and double reduction, but the evidence suggests that incompatibility factors derived from the wild species employed in the breeding work had a selective influence on the union of gametes, and hence on the distribution of resistants and susceptibles in the progenies.

A feature of the experiments was the similarity of the segregation ratios observed in progenies in A-resistant material tested with strain A on the one hand, and in progenies in B-resistant material tested with strain B on the other.

The presence of the Ra gene was found to provide no appreciable protection against attack by the B strain, since plants possessing it gave reactions similar in intensity to the recessive forms.

The experiments to be discussed in this report are primarily concerned with the C strain of the parasite. This strain appeared on a seedling,

877*a*(34), which was known to be resistant to strains A and B. The family tree of 877*a*(34) (fig. 1) shows that only two species were employed in its production, viz. *S. demissum* and *S. tuberosum*. The variety of *S. demissum* here referred to is the same as that used in the previous experiments, and is now included in the Commonwealth Potato Collection under the Reference No. CPC 2127.

Experimental Results

For convenience, the blight-resistant seedlings employed as parents in the breeding work to be discussed are listed in Table I, and their reactions to the three strains of blight, A, B and C, are shown. It will

Table I.—Reactions to Strains A, B and C of *S. demissum* Derivatives used as Parents

Ref. No.	Reaction to Strain			Ref. No.	Reaction to Strain		
	A	B	C		A	B	C
653*c*(35)	R	S	R	1092*a*(4)	R	S	R
655(43)	R	S	R	1253*a*(12)	R	R	R
W.800(2)	R	S	R	1270*b*(9)	R	R	R
834*b*(6)	R	S	R	1271*b*(11)	R	R	R
834*c*(29)	R	S	R	1306*a*(2)	R	R	R
835*a*(4)	R	S	R	1315*b*(10)	R	R	S
877*a*(34)	R	R	S	1318(3)	R	R	S
882(5)	R	R	R	1332*a*(6)	R	R	R

R = Resistant. S = Susceptible.

be noted that all are resistant to strain A, but in relation to B and C three different resistant phenotypes are present, viz.

(1) Plants resistant to B but susceptible to C.
(2) ,, ,, ,, C ,, ,, ,, B.
(3) ,, ,, ,, both B and C.

In Table II are shown the segregations obtained in progenies derived from 877*a*(34) and 1318(3) (fig. 1) where all three strains, A, B and C, were separately employed. The female parent in the crosses is a recessive type in each case.

Seedling 877*a*(34) is resistant to strains A and B but susceptible to C. The progeny from which it was selected, viz. 877, was tested with strain A (Black, 1943, Table VII), and segregated 129 resistants : 130 susceptibles—a close approximation to a 1 : 1 ratio. A further quantity

TABLE II.—DERIVATIVES OF 877*a*(34) TESTED WITH STRAINS A, B AND C

Ref. No.	Parentage	Strain	Number of Seedlings		Ratio		Suggested Genotypes (Dominant Genes only)
			R	r	Observed	Theoretical	
1330*a*	877*a*(34) N.S.	A	111	26	4·27 : 1	3 : 1	Rb
1315*abc*	Epicure × 877*a*(34)	A	301	336	0·90 : 1	1 : 1	Recessive × Rb
1318	Craigs Defiance × 877*a*(34)	A	74	89	0·83 : 1	1 : 1	
1321*abc*	Ninetyfold × 877*a*(34)	A	142	199	0·71 : 1	1 : 1	
			517	624	0·83 : 1		
1444	British Queen × 877*a*(34)	B	29	30	0·97 : 1	1 : 1	Recessive × Rb
1648*ab*	Southesk × 1318(3)	B	148	177	0·84 : 1	1 : 1	
1650, 1651*a*	831(113) × do.	B	156	183	0·85 : 1	1 : 1	
			333	390	0·85 : 1		
1619*c*	877*a*(34) N.S.	C	0	99	..	0 : 00	Rb
1727*a*	1318(3) N.S.	C	1	173	..	0 : 00	

N.S. = Natural Self.

of seed from the same cross (Ref. No. 877*d*) was sown to provide plants for C strain test. Eighty-seven seedlings were inoculated and all proved to be susceptible. It is apparent from these results that 877*a*(34) possesses the gene Rb in the simplex condition, and that it should, on crossing with recessive types, give progenies which segregate resistants and susceptibles in equal proportions, irrespective of whether the A or the B strain of the fungus is used. This is confirmed in Table II. Seedling 1318(3), which was bred from 877*a*(34), gave similar results in the B strain tests but was not included in the experiments with strain A.

Further confirmation of the presence of the gene Rb was obtained from selfed progenies of 877*a*(34), in which a ratio of 3 resistants : 1 susceptible resulted from inoculation with strain A, but with strain C all the individuals proved to be susceptible. The selfed progeny of 1318(3) was also expected to succumb to strain C, and 173 of the 174 plants did so. It is probable that the single survivor was a rogue plant arising from contamination by foreign pollen of the unprotected flower.

These results show that, with reference to strains A, B and C, 877*a*(34) and 1318(3) possess the gene Rb, which confers resistance to strains A and B but not to C.

In earlier experiments, seedling W.800(2) proved to be resistant to strain A but susceptible to strain B, and was believed to possess the gene

Ra (Black, 1945, Table V). When this seedling and several of its resistant descendants were subjected to infection with the C strain, they exhibited the same resistance as they did to strain A. Accordingly a number of progenies, obtained by crossing W.800(2) and some of its derivatives with recessive varieties, were tested with the C strain in order to compare the segregations with these previously observed in the A strain experiments (*e.g.* Black, 1949, Table XIII). The segregations in the C strain tests are shown in Table III. They approximate to a 1 : 1 ratio, deviating

TABLE III.—DERIVATIVES OF W.800(2) TESTED WITH STRAIN C

Ref. No.	Parentage	Number of Seedlings		Ratio		Suggested Genotypes (Dominant Genes only)
		R	r	Observed	Theoretical	
835*b*	Craigs Defiance × W.800(2)	75	94	0·80 : 1	1 : 1	Recessive × Rc
1411*a*	Majestic × 834*b*(6)	31	29	1·07 : 1	1 : 1	
1412*e*	do. × 834*c*(29)	90	150	0·60 : 1	1 : 1	
1415*b*	653*c*(35) × Katahdin	102	103	0·99 : 1	1 : 1	Rc × Recessive
1416*b*	do. × Dr McIntosh	57	71	0·80 : 1	1 : 1	
1417*e*	do. × 910*a*(123)	42	63	0·67 : 1	1 : 1	
1418*e*	655(43) × Katahdin	24	32	0·75 : 1	1 : 1	
1419*d*	do. × Dr McIntosh	39	53	0·74 : 1	1 : 1	
1423*a*	834*b*(6) × Katahdin	158	129	1·22 : 1	1 : 1	
1425*b*	835*a*(4) × do.	81	83	0·98 : 1	1 : 1	
		699	807	0·87 : 1	1 : 1	

steadily towards an excess of recessives, and are comparable with the ratios previously obtained with the A strain of the fungus.

That resistance is due to the presence of one major gene is confirmed by the fact that no seedling which survived the A strain test was found to be susceptible to C, and similarly no survivor of the C strain test proved to be susceptible to strain A. In view of these findings, the gene carried by W.800(2) and inherited by its resistant offspring must now be designated Rc.

The intercrossing of Rb plants (Table II) with Rc plants (Table III) might be expected to produce three different resistant genotypes in the offspring. Tests of such progenies with strains B and C independently (Table IV) show that in both cases the segregations approximate equality. When, however, the survivors of the B strain test are inoculated with strain C, approximately half of their number succumb (Table V). Similarly when the survivors of the C strain test are inoculated with strain B approximately half of their number are killed (Table VI). Apparently the plants segregate in the proportion of 1 RbRc : 1 Rbrc : 1 rbRc : 1 rbrc.

TABLE IV.—DERIVATIVES OF 877*a*(34) AND W.800(2) TESTED WITH STRAINS B AND C

Ref. No.	Parentage	Strain	Number of Seedlings		Ratio		Suggested Genotypes (Dominant Genes only)
			R	r	Observed	Theoretical	
1647*ab*	655(43) × 1318(3)	B	38	53	0·72 : 1	1 : 1	Rc × Rb
1658*a*, 1659*a*	835*a*(4) × do.	B	166	146	1·14 : 1	1 : 1	Rc × Rb
1678*ab*	1092*a*(4) × do.	B	105	111	0·95 : 1	1 : 1	Rc × Rb
1697*a*	1315*b*(10) × 834*c*(29)	B	93	90	1·03 : 1	1 : 1	Rb × Rc
			402	400	1·01 : 1		
1659*c*	835*a*(4) × 1318(3)	C	104	95	1·09 : 1	1 : 1	Rc × Rb
1678*c*	1092*a*(4) × do.	C	52	50	1·04 : 1	1 : 1	Rc × Rb
1697*b*	1315*b*(10) × 834*c*(29)	C	149	161	0·93 : 1	1 : 1	Rb × Rc
			305	306	1·00 : 1		

If strain B is applied first, the rbRc and the recessives individuals are killed. Subsequent inoculation of the survivors with strain C destroys the Rbrc plants, leaving only the RbRc types alive. When the order of

TABLE V.—DOUBLE TEST (STRAIN B FOLLOWED BY STRAIN C)

Ref. No.	Parentage		Killed by		Survived	Suggested Genotypes (Dominant Genes only)
			B	C		
1647*ab*	655(43) × 1318(3)	O	53	19	19	Rc × Rb
		E	45·5	22·75	22·75	
1658*a*	835*a*(4) × 1318(3)	O	81	33	53	Rc × Rb
		E	83·5	41·75	41·75	
1678*a*	1092*a*(4) × 1318(3)	O	66	33	28	Rc × Rb
		E	63·5	31·75	31·75	
1697*a*	1315*b*(10) × 834*c*(29)	O	90	45	48	Rb × Rc
		E	91·5	45·75	45·75	

O = observed. E = expected.

inoculation is reversed, the C strain kills the Rbrc and the recessive plants, while the B strain destroys the rbRc types. Again only the RbRc segregates, representing approximately 25 per cent. of the original progeny, remain alive.

Seedling progenies, obtained by crossing triple hybrid derivatives (Black, 1949, Table I) with the Rb types 1318(3) and 1315*b*(10), were

TABLE VI.—DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B)

Ref. No.	Parentage		Killed by		Survived	Suggested Genotypes (Dominant Genes only)
			C	B		
1659*c*	835*a*(4) × 1318(3)	O	95	52	52	Rc × Rb
		E	99·5	49·75	49·75	
1678*c*	1092*a*(4) × 1318(3)	O	50	27	25	Rc × Rb
		E	51	25·5	25·5	
1697*b*	1315*b*(10) × 834*c*(29)	O	161	70	79	Rb × Rc
		E	155	77·5	77·5	

O = observed. E = expected.

tested with strains B and C as indicated in Table VII. The triple hybrid derivatives employed as parents, viz. 1253*a*(12), 1270*b*(9), 1271*b*(11) and 1332*a*(6), were previously credited with the gene Rb (Black, 1945, Table

TABLE VII.—DERIVATIVES OF 877*a*(34) AND TRIPLE HYBRIDS TESTED WITH STRAINS B AND C

Ref. No.	Parentage	Strain	Number of Seedlings		Ratio		Suggested Genotypes (Dominant Genes only)
			R	r	Observed	Theoretical	
1682*ab*	1253*a*(12) × 1318(3)	B	109	35	3·11 : 1	3 : 1	Rbc × Rb
1691*a*	1270*b*(9) × do.	B	140	44	3·18 : 1	3 : 1	Rbc × Rb
1696	1271*b*(11) × do.	B	225	71	3·17 : 1	3 : 1	Rbc × Rb
1698*a*	1315*b*(10) × 1306*a*(2)	B	111	43	2·58 : 1	3 : 1	Rb × RaRbc
1699	do. × 1332*a*(6)	B	194	73	2·66 : 1	3 : 1	Rb × Rbc
			779	266	2·93 : 1		
1691*b*	1270*b*(9) × 1318(3)	C	121	138	0·88 : 1	1 : 1	Rbc × Rb
1698*c*	1315*b*(10) × 1306*a*(2)	C	82	102	0·80 : 1	1 : 1	Rb × RaRbc
			203	240	0·85 : 1		

II; 1949, Tables III and X), but since they have proved resistant to strain C as well as to strain B, a new gene must be postulated, viz. Rbc. Similarly 1306*a*(2), which was previously described as having the two genes RaRb (Black, 1949, Table X), must now be represented by RaRbc. Against strains B and C the Ra gene is, of course, ineffective and may be ignored.

The intercrossing of Rb and Rbc genotypes thus gives progenies which segregate in the ratio of approximately 3 resistants : 1 susceptible when tested with strain B, and approximately in equal proportions when tested with strain C. These results would be expected since both parents are B resistant but only one of them is C resistant.

As shown in Table VIII, approximately 25 per cent. of the individuals

TABLE VIII.—DOUBLE TEST (STRAIN B FOLLOWED BY STRAIN C)

Ref. No.	Parentage		Killed by		Survived	Suggested Genotypes (Dominant Genes only)
			B	C		
1691*a*	1270*b*(9) × 1318(3)	O	44	37	103	Rbc × Rb
		E	46·0	46·0	92·0	
1696	1271*b*(11) × 1318(3)	O	71	70	155	Rbc × Rb
		E	74·0	74·0	148·0	
1699	1315*b*(10) × 1332*a*(6)	O	73	68	126	Rb × Rbc
		E	66·75	66·75	133·5	
1698*a*	1315*b*(10) × 1306*a*(2)	O	43	35	76	Rb × RaRbc
		E	38·5	38·5	77·0	

O = observed. E = expected.

are killed by the B strain. Subsequent inoculation of the survivors with strain C destroys approximately one-third of the B resisters. When the C strain is used first, however, approximately half of the plants are killed by it (Table IX), and the remainder are unaffected by exposure to strain B.

TABLE IX.—DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B)

Ref. No.	Parentage		Killed by		Survived	Suggested Genotypes (Dominant Genes only)
			C	B		
1691*b*	1270*b*(9) × 1318(3)	O	138	..	121	Rbc × Rb
		E	129·5	..	129·5	
1698*c*	1315*b*(10) × 1306*a*(2)	O	102	..	82	Rb × RaRbc
		E	92	..	92	

O = observed. E = expected.

This evidence indicates that the progenies segregate in the ratio of approximately 1 RbRbc : 1 Rbrbc : 1 rbRbc : 1 rbrbc. Strain B can kill only the recessives (25 per cent.), while strain C is effective against the

Rbrbc segregates (25 per cent.) as well as the recessives. In these progenies, therefore, the C strain alone gives the same results as would a mixture of the two strains B and C, and the only plants which would survive would be those possessing the Rbc gene with or without the help of the Rb gene.

Discussion

Potato varieties resistant to blight fall into three distinct phenotypic groups, viz.

(1) Plants resistant to strains A and B but susceptible to strain C.
(2) ,, ,, ,, ,, A and C ,, ,, ,, ,, B.
(3) ,, ,, ,, ,, A, B and C.

Thus all plants which are resistant to B or to C are also resistant to A. This suggests that strain A, in power of attack, is less virulent than either of the specialised strains B or C. But the difference between B and C cannot be expressed in degree of virulence, since one plant may be B resistant–C susceptible while another may be B susceptible–C resistant. The difference is one of quality, and the two strains must be regarded as differing in type of pathogenicity rather than in degree of virulence. The modes of origin of strains B and C are not known, but since sexual reproduction in *P. infestans* has not been observed in nature, it seems certain that hybridity is not involved and that probably both arose from the common strain A by somatic mutation. The two mutants are widely divergent in character.

Mutants of the C type appeared less frequently than those of the B type. In preliminary tests carried out with seven different strains, six of them differed from each other only in degree of virulence, and formed a series ranging from low degree to high degree of pathogenicity. In such a series, a plant susceptible to any one strain is susceptible to all strains of greater virulence, and, conversely, a plant resistant to any one strain is resistant to all strains of lesser virulence. The individuals of this series, which includes strain B, thus show only quantitative differences in virulence. The remaining strain, viz. C, is not classifiable in this series and must represent a separate group. As already shown, it differs from the B group by virtue of the quality and not the degree of its infective power. This preponderance of strains of the B group may be due to the breeding, unwittingly, of a greater range of genotypes capable of isolating such mutants.

Since neither of the specialised strains B or C has been found in commercial crops of ordinary varieties (Black and Haigh, 1947; Keay,

1949), the blight population associated with such crops may be presumed to be more or less uniform in infective power. Recorded cases of fungal specialisation invariably occurred at or near potato-breeding centres, where a range of resistant plants provided the corpus on which the specialised fungus declared itself. If such mutants do occur in ordinary crops, they must be unable to persist in the field in open competition with the established form.

The common or A strain of the blight fungus may best be regarded as a comparatively unstable population maintained at an equilibrium compatible with the constitution of the potato varieties with which it is in contact. Mutations may frequently occur, but mutant forms will tend to disappear unless host plants, to which they are specially adapted, are available. It has been shown by Reddick and Mills (1938) and de Bruyn (1947) that a strain may quickly lose its identity in a heterogeneous collection of resistant varieties. This instability has been confirmed by the writer on two occasions (Black, 1947 and 1949). In the first case, blight appeared on a seedling which was resistant to strain A, but it failed to attack the filter varieties normally used for B and C. In degree of virulence, this strain, designated D, appeared to be intermediate between either A and B or A and C. Repeated inoculations of detached leaves of the B and C filter plants were made, until eventually a few conidia were observed on the C filter plant. After four passages through leaves of this plant, the reaction obtained was similar to that produced by strain C. Strain D was therefore regarded as a weak relative of strain C. In the second case, an increase in the virulence of strain B was discovered when the segregation ratios of certain matings unexpectedly changed in character. The new ratios showed a higher proportion of susceptibles than the old, although the reactions of the parents were unaltered. It happened that the resistant parents had two independent genes, both of which conferred resistance to the original B strain, but only one of them to the parasite in its more virulent state.

Although these changes in infective power are all towards increase, it is reasonable to assume that other mutants arise with a corresponding decrease in power of attack. Such a decrease, however, would be difficult to demonstrate, because selection for resistance in potato varieties has naturally been in the upward direction, and decreased virulence in the parasite would not be detected under ordinary circumstances. It has been found, however, that specialised strains can be maintained at a constant level of virulence, provided the varieties upon which they originally appeared are used as hosts.

In the experiments described above no differences were observed in

the nature of the reactions of the resistant seedlings to the available biotypes of the fungus. In all cases the leaves showed local necrotic lesions, demonstrating a first penetration of the parasite and then its early death.

The physiology of this defence reaction has been examined by Müller (1941), Müller and Boerger (1941) and Müller and Behr (1949), who concluded that resistance genes function only as accelerators of the reaction which the susceptible genotypes are also capable of producing. They found that no fundamental, but only a graduated, difference between resistants and susceptibles existed. Thus the greater the speed of reaction the greater would be the degree of resistance of the plant. These conclusions appear to be well founded in relation to infection with a single strain of the parasite, but where two strains such as B and C are concerned, speed of reaction alone cannot explain the difference in resistance exhibited by the foliage of 877*a*(34) (gene Rb) and W.800(2) (gene Rc). This difference is qualitative in character, and therefore the respective genes involved must control some resistance mechanism other than, or in addition to, speed of reaction.

As shown in Table X, the segregations of resistants from susceptibles

TABLE X.—TOTALS FROM PREVIOUS TABLES

Source of Data	Genotypes Involved	Strain	Number of Seedlings		Ratio	
			R	r	Observed	Theoretical
Table II	Rb and Recessive	A	517	624	0·83 : 1	1 : 1
,, ,,	,, ,, ,,	B	333	390	0·85 : 1	1 : 1
Black (1949, Table VIII)	Rc and Recessive	A	5730	6842	0·85 : 1	1 : 1
Table III	,, ,, ,,	C	699	807	0·87 : 1	1 : 1
Table IV	Rb and Rc	B	402	400	1·005 : 1	1 : 1
,, ,,	,, ,, ,,	C	305	306	1·00 : 1	1 : 1
Table VII	Rb and Rbc	B	779	266	2·93 : 1	3 : 1
,, ,,	,, ,, ,,	C	203	240	0·85 : 1	1 : 1

in progenies involving only the Rb gene were almost identical, irrespective of whether strain A or strain B was employed for inoculation. Similarly in progenies involving only the Rc gene, the A strain was as effective as the C strain in differentiating the resistant individuals. In these progenies,

where one of the parents in each case was a recessive, a significant deviation in favour of recessives from the standard 1 : 1 ratio was observed. When Rb plants were crossed with Rc plants, the segregations resulting from inoculation with the B strain were comparable with those obtained from C strain infection. These segregations, however, showed no appreciable deviation from the standard 1 : 1 ratio. Thus deviations appeared when *S. tuberosum* plants were crossed with *S. demissum* derivatives, but were less conspicuous in the progenies bred from *S. demissum* derivatives only. This suggests that the unbalanced segregations commonly found in species-crosses may disappear when plants of similar origin are intercrossed, and that the phenomenon is due to a selective effect at the time of fertilisation, caused by the action of incompatibility factors. The results of Rb × Rbc progenies tested with strain C show a greater deviation from the 1 : 1 ratio than expected, but the number of plants tested are not sufficiently large to be conclusive. It seems reasonable to assume, however, that incompatibility factors may be operative even in the mating of species hybrid derivatives of similar origin, and that the extent of the deviations from standard segregation ratios will depend upon the balance of incompatibility genes in the constitution of the parents involved.

Summary

1. The two specialised strains of *Phytophthora infestans*, designated B and C, are alike in that both are more virulent than the common strain A; they differ from each other in a qualitative manner. Each probably arose from strain A by mutation.

2. Strains B and C are representatives of two distinct groups, within each of which only differences in degree of virulence appear to exist. The majority of new strains examined were members of the B group.

3. Under test conditions, specialised strains of blight may alter in virulence, but each can be maintained in continuous culture on a host plant to which it is specially adapted without appreciable change.

4. In the present experiments the following genes in the host are postulated as controlling resistance: Rb, conferring resistance to strains A and B; Rc, conferring resistance to strains A and C; Rbc, conferring resistance to strains A, B and C. Each gene is independent of the other in producing its effect, and is inherited independently in simple Mendelian fashion.

5. Deviations from standard Mendelian ratios were consistent in their trend when *S. tuberosum* plants were crossed with resistant hybrid derivatives of *S. demissum*. In contrast, these unbalanced segregations

were much less in evidence when such derivatives of *S. demissum* were intercrossed. The departure from Mendelian expectations may be due to some relationship between the genes affecting disease resistance and incompatibility genes.

Grateful acknowledgment is made to Dr Alexander Nelson for advice and criticism, and to Dr J. C. Haigh for assistance in the work.

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XVII.—Inheritance of Resistance to Blight (*Phytophthora infestans*) in Potatoes: Inter-Relationships of Genes and Strains.*

By **William Black,** B.Sc., Ph.D., Scottish Plant Breeding Station, Corstorphine, Edinburgh. (With Six Text-figures.)

(MS. received March 9, 1951. Read July 2, 1951)

Synopsis

The common strain and six specialised strains of *Phytophthora infestans* have been employed in testing potato varieties and seedling progenies bred from the wild species *S. demissum* for resistance to the disease. Resistance, due to the hypersensitive condition of the protoplasm, is manifested in the presence of major genes, and four such genes have been identified, viz. R_1, R_2, R_3 and R_4. Each gene induces in the plant a hypersensitive response to infection with the common strain and with a particular group of specialised strains of the parasite. The genes are inherited independently in simple Mendelian fashion, but in the segregations three different types of deviations from standard disomic ratios occur due to (*a*) unpaired chromosomes, (*b*) incompatibility factors, and (*c*) partial autosyndesis. A series of minor genes modify the phenotypic expression of the major gene system and so differentiate grades of hypersensitivity or of susceptibility as the case may be.

The common strain of *P. infestans* appears to be a population persisting at an equilibrium determined by host range and environmental conditions. Mutations frequently occur, but new forms survive only when host genotypes, to which they are specially adapted, are available.

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Introduction

Previous reports (Black, 1943, 1945, 1949 and 1950) of experiments relating to the inheritance of resistance to blight (*Phytophthora infestans*) in the potato were concerned with the reactions of hybrid seedlings and seedling progenies to infection with the common strain A and two specialised strains B and C of the parasite. From the accumulated information the following conclusions were reached:—

(1) The resistance exhibited by *S. demissum* and seedlings bred from it is due primarily to the hypersensitive condition of the protoplasm.

* This paper was assisted in publication by a grant from the Carnegie Trust for the Universities of Scotland.

(2) The hypersensitive condition is manifested in the presence of one or more major genes, of which three were identified.

(3) Each major gene confers resistance to the common strain and to certain specialised strains and is inherited in simple Mendelian fashion.

(4) A series of minor genes, associated with various morphological and physiological characters, are capable of modifying the phenotypic expression of major genes and thereby differentiating degrees of resistance and of susceptibility.

(5) In the early generations of *S. demissum* and *S. tuberosum* hybrids, the irregularity of chromosome behaviour and the presence of unpaired chromosomes caused the ratios of resistants to susceptibles to vary widely from standard Mendelian ratios.

(6) The consistent excess of recessive individuals observed in certain progenies bred from apparently cytologically normal parents appeared to be due to the influence of minor incompatibility factors introduced from the gene complex of *S. demissum*.

(7) New specialised strains of *Phytophthora* arise mainly by mutation, but the possible effect of hybridisation in this connection cannot be ruled out.

(8) Specialisation is not limited to simple degrees of virulence, but may occur in widely different directions resulting in qualitatively different races.

(9) The so-called common strain of the fungus persists under natural conditions because it is the race best adapted to existing climatic conditions and to the varieties commonly grown. New strains are frequently produced, but these survive only when the appropriate host genotypes to which they are specially adapted are available.

(10) Specialised strains are not more destructive of the host tissues than the common strain when on ordinary commercial varieties. They may be maintained over the years without significant change on plants of the genotype to which they are specially adapted.

These experiments have been continued and their scope has been widened by the isolation of additional strains of the pathogen and the production of further generations of seedling progenies. The present paper attempts to explain the inheritance of resistance to seven different strains and to provide a concise genetical interpretation of the data presented in this and in the previous reports.

Materials and Methods

The plants employed for test purposes were derived from four main breeding systems, viz.:

(1) *Multiple Hybrid.*—The earlier generations were produced by the late Dr Wilson, St Andrews, who made the initial crosses over forty years ago (fig. 1). The writer received seedling W800(2) for breeding purposes, but as far as he is aware no critical tests for resistance to blight were made in any of the preceding

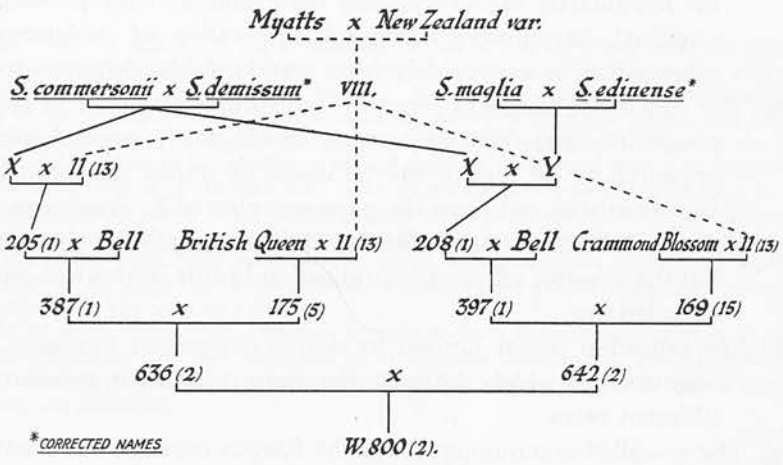

Fig. 1.

generations. The variety of *S. demissum* employed by Dr Wilson cannot be identified with certainty, but it is probable, in view of the limited material available at the time, that it was the same as that employed by the writer in the remaining three schemes of breeding. This variety is now included in the Commonwealth Potato Collection under the reference CPC 2127.

(2) *S. demissum–S. tuberosum Hybrids.*—The original cross of this material was made in 1932 using variety CPC 2127 of *S. demissum*. The family tree is shown in fig. 2. The early generations showed irregularities in chromosome behaviour. Seedling 877*a*(34), however, appeared to be normal and was widely employed as a parent.

(3) *S. Rybinii–S. demissum–S. tuberosum Hybrids.*—The original cross was made in 1937 from *S. Rybinii* CPC 1311 and *S. demissum* CPC 2127. Chromosome behaviour was regular

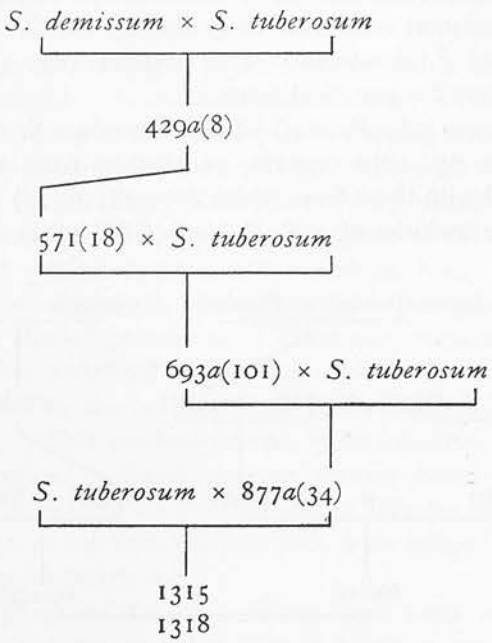
S. demissum × S. tuberosum
429a(8)
571(18) × S. tuberosum
693a(101) × S. tuberosum
S. tuberosum × 877a(34)
1315
1318

FIG. 2.

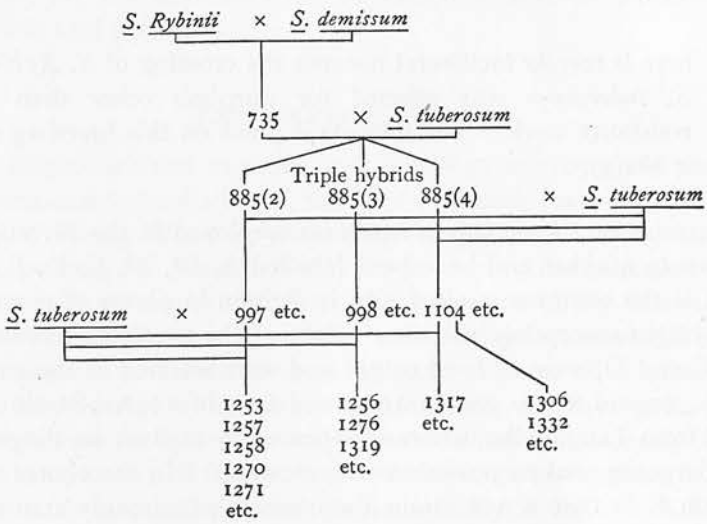
S. Rybinii × S. demissum
735 × S. tuberosum
Triple hybrids
885(2) 885(3) 885(4) × S. tuberosum
S. tuberosum × 997 etc. 998 etc. 1104 etc.
1253
1257
1258
1270
1271
etc.
1256
1276
1319
etc.
1317
etc.
1306
1332
etc.

FIG. 3.

throughout (Thomas, 1945), due to the initial synthesising of a blight-resistant tetraploid from the diploid *S. Rybinii* and the hexaploid *S. demissum*. This material (fig. 3) proved highly satisfactory for genetical work.

(4) (*S. tuberosum* × *S. Rybinii*) × (*S. demissum* × *S. tuberosum*).—As shown in fig. 4 the first two generations from *S. demissum* are identical with those from which 877*a*(34) (fig. 2) was bred. This pedigree includes also *S. Rybinii* (CPC 1311), but its presence

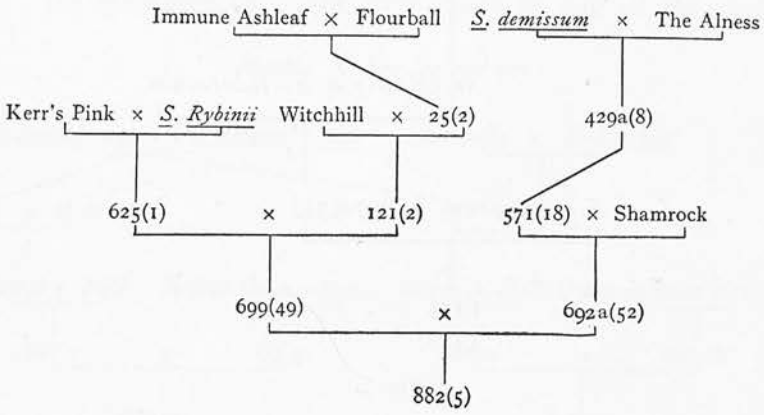

FIG. 4.

here is merely incidental because the crossing of *S. Rybinii* and *S. tuberosum* was effected for purposes other than blight-resistance work. The important plant on this breeding scheme is 882(5).

The strains of *Phytophthora infestans* employed in the investigations were seven in number and have been labelled A, B^1, B^2, C, D, E and F. Strain A is the common strain found in Britain in plants of commercial crops of blight-susceptible varieties. Four of the specialised strains, viz. B^1, B^2, C and D, were of local origin and were isolated in the course of the work, one in 1939, one in 1944 and two in 1947. Strain E was obtained from Tanganyika, where it appeared in 1948 on seedlings which were undergoing trial as possible economic types. In the course of tests with strain E in 1949 a new strain F appeared, presumably arising from the Tanganyika strain by mutation.

The method employed in the routine tests of seedling progenies was devised to provide approximately the optimum conditions for the growth

of the parasite, viz. a temperature of 19° C. with relative humidity approaching 100 per cent. The temperature was controlled by using a glasshouse fitted with adequate heating and ventilation and a shading device to exclude direct sunlight. To maintain the necessary humidity the seedlings to be tested were transplanted into boxes containing moist sterilised peat, and these in turn were placed in a shallow tank with a close-fitting lid. In that position the seedlings were sprayed, by means of an atomiser, with a spore suspension of the appropriate strain of the fungus. The lid was then closed. After approximately sixteen hours the boxes were removed from the tank and the plants exposed to the ordinary atmospheric conditions of the shaded glasshouse. There they remained for about five days, when lesions appeared on the susceptible segregates. The boxes were then replaced in the tank to promote abundant sporulation and so facilitate scoring. This method proved to be effective in killing off the susceptible segregates without causing serious harm to the resistant survivors. The latter may be retested with a different strain if so desired. At the completion of the tests the survivors were transplanted and grown to maturity in the ordinary way.

For certain purposes detached leaves were used instead of plants. The leaves were laid flat on moist peat in boxes, sprayed as before and covered with a suitable lid. They remained in this position for about seven days, when they were ready for scoring. This method is very convenient for the multiplication of fungal strains on leaves of their appropriate host plants.

Experimental Results

The blight-resistant varieties and seedlings employed as parents in the experiments to be discussed, together with their reactions to the seven biotypes of *Phytophthora infestans* and the genes which they have been found to possess, are listed in Table I. In view of the increased number of strains and the impracticability of referring to all by designation of genes, it is inevitable that a modified system of gene nomenclature must be formulated. The method now adopted consists of numbering the genes in the order in which they were identified, viz. R_1, R_2, R_3 and R_4. Examination of the reactions will reveal that the relationship between genes in the potato and fungus strains forms a definite pattern which, to facilitate reference, is illustrated diagramatically in fig. 5. A line connecting a gene with a strain indicates that the gene, when present, confers resistance to that strain.

It has been previously shown (Black, 1945, Tables V, VI, VII, VIII;

TABLE I.—REACTIONS TO SEVEN STRAINS OF RESISTANT VARIETIES AND SEEDLINGS USED AS PARENTS

Reference	Reaction to Strains							Genotypes (Significant Terms only)
	A	B^1	B^2	C	D	E	F	
Aquila	R	s	s	R	R	s	s	R_1
Jakobi	R	s	s	R	R	s	s	R_1
Kennebec	R	s	s	R	R	s	s	R_1
W.800(2)	R	s	s	R	R	s	s	R_1
735	R	R	R	R	R	R	R	$R_1R_2R_3R_4$
834*b*(6)	R	s	s	R	R	s	s	R_1
834*c*(29)	R	s	s	R	R	s	s	R_1
835*a*(4)	R	s	s	R	R	s	s	R_1
877*a*(34)	R	R	R	s	R	R	R	R_2
882(5)	R	R	R	R	R	R	R	R_1R_2
885(2)	R	R	R	R	R	s	s	R_1R_3
885(4)	R	R	R	R	R	R	s	$R_1R_3R_4$
886(1)	R	R	R	s	R	R	R	R_2R_4
914*a*(12)	R	s	s	R	R	s	s	R_1
914*a*(91)	R	s	s	R	R	s	s	R_1
914*b*(52)	R	s	s	R	R	s	s	R_1
997*a*(51)	R	R	R	R	R	s	s	R_3
1104*a*(3)	R	R	R	R	R	R	s	R_3R_4
1104*c*(2)	R	R	R	R	R	R	s	R_3R_4
1253*a*(12)	R	R	R	R	R	s	s	R_3
1253*a*(15)	R	R	R	R	R	s	s	R_3
1256*a*(23)	R	R	R	R	R	s	s	R_3
1258*a*(19)	R	R	R	R	R	s	s	R_3
1270*b*(9)	R	R	R	R	R	s	s	R_3
1276*b*(6)	R	R	R	R	R	s	s	R_3
1276*b*(10)	R	R	R	R	R	s	s	R_3
1306*a*(2)	R	R	R	R	R	R	s	R_3R_4
1306*a*(15)	R	R	R	R	R	R	s	$R_3R_3R_4$
1307*a*(23)	R	R	R	R	R	s	s	R_3R_3
1315*b*(10)	R	R	R	s	R	R	R	R_2
1318(3)	R	R	R	s	R	R	R	R_2
1439*a*(4)	R	R	R	R	R	s	s	R_3
1488*b*(1)	R	R	R	R	R	R	s	R_3R_4
1508*b*(3)	R	R	R	s	R	R	R	R_2
1509*a*(3)	R	R	R	s	R	R	R	R_2
1509*a*(4)	R	R	R	s	R	R	R	R_2
1512*c*(14)	R	R	R	s	R	R	R	R_2
1512*d*(4)	R	R	R	R	R	R	R	$R_1R_1R_2$
1514*a*(1)	R	R	R	R	R	R	R	R_1R_2
1517*a*(1)	R	R	R	s	R	R	R	R_2
1517*b*(2)	R	R	R	R	R	R	R	R_1R_2
1518*d*(2)	R	R	R	s	R	R	R	R_2R_4
1521*c*(6)	R	R	R	R	R	R	R	$R_2R_3R_4$
1563*a*(5)	R	R	R	R	R	s	s	R_3
1563*a*(6)	R	R	R	R	R	s	s	R_3
1563*a*(18)	R	R	R	R	R	s	s	R_3
1563*b*(8)	R	R	R	R	R	R	s	R_3R_4
1564*a*(9)	R	R	R	R	R	R	s	R_3R_4
1564*a*(12)	R	R	R	R	R	R	s	R_3R_4
1567*a*(7)	R	R	R	R	R	R	s	R_3R_4
1584*b*(7)	R	R	R	R	R	R	s	R_3R_4
1591*a*(19)	R	R	R	R	R	R	s	R_3R_4

R = resistant. s = susceptible.

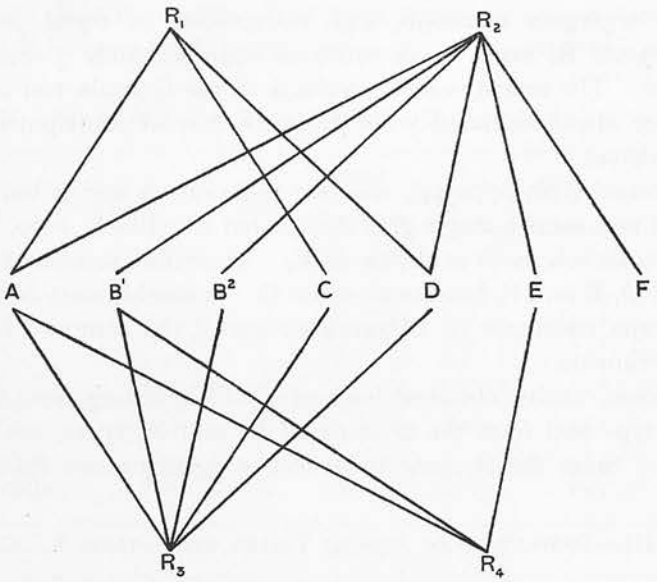

FIG. 5.

1949, Table XIII; 1950, Tables III, IV, V, VI) that seedling W800(2) and its resistant derivatives possess a gene conferring resistance to strains A and C. This gene, originally named Ra and later renamed Rc when it was found to provide protection against both the A and C strains of the pathogen, is now designated R_1. In relation to the seven strains now employed, R_1 types are resistant to strains A, C and D and susceptible to B_1, B_2, E and F. Gene R_1 has been found not only in W800(2) lines, but also in triple hybrid material, in *S. demissum–S. tuberosum* derivatives, in German crop varieties, *e.g.* Aquila, and similarly in American varieties, *e.g.* Kennebec.

Further segregations involving the gene R_1 are shown in Table II, where strain C was employed for test purposes. Seedling 834*c*(29) and Aquila are the R_1 types, and when these are crossed with recessives the

TABLE II.—DERIVATIVES OF MULTIPLE HYBRID W.800(2) AND OF AQUILA TESTED WITH STRAIN C. GENE R_1

Ref. No.	Parentage	Number of Seedlings		Ratio		Genotypes (Significant Terms only)
		R	r	Observed	Theoretical	
1481*d*	791*a*(116) × 834*c*(29)	52	58	0·90 : 1	1 : 1	$r \times R_1$
1906*ab*	King Edward VII × Aquila	32	43	0·74 : 1	1 : 1	$r \times R_1$
1978*ab*	Aquila Selfed	195	51	3·82 : 1	3 : 1	R_1

progenies segregate resistants and susceptibles in equal proportions. The selfing of R_1 types gives ratios of approximately 3 resistants : 1 susceptible. The seventy-seven survivors of the C strain test in progeny 1978*a* were also inoculated with strain D, but as anticipated they all proved resistant.

The second type, 877*a*(34), resistant to strains A and B but not to C, was found to possess a single gene designated Rb (Black, 1950, Table II). In the present scheme it is shown as R_2. It confers resistance to strains A, B^1, B^2, D, E and F, but not to strain C. A combination of R_1 and R_2 thus provides resistance to all seven strains of the fungus employed in these experiments.

Additional results, obtained from progenies resulting from the selfing of an R_2 type and from the crossing of R_1 and R_2 types, are shown in Table III. Since the R_1 gene is ineffective against strain E, the simple

TABLE III.—DERIVATIVES OF 877*a*(34) TESTED WITH STRAIN E. GENE R_2

Ref. No.	Parentage	Number of Seedlings		Ratio		Genotypes (Significant Terms only)
		R	r	Observed	Theoretical	
1979*ab*, 1818*a*	877*a*(34) Selfed	148	68	2·18 : 1	3 : 1	R_2
1660*ab*	835*a*(4) × 1318(3)	157	146	1·08 : 1	1 : 1	$R_1 \times R_2$
1697*c*	1315*b*(10) × 834*c*(29)	99	88	1·13 : 1	1 : 1	$R_2 \times R_1$
		256	234	1·09 : 1		

3 : 1 segregations for selfs and 1 : 1 for crosses were obtained. These results are similar to those previously obtained with strain B^2. The ninety-four plants of progeny 1979*ab* which survived the E strain test were later inoculated with strain F, but all, as expected, proved to be resistant.

The third type of resister, exemplified by 1253*a*(12) of triple hybrid origin, was selected from family 1253 (Black, 1945, Table II). It was found to possess one gene conferring resistance to strains A and B and was regarded as an Rb type. Later (Black, 1950, Table VII), it proved to be resistant also to strain C and the gene was renamed Rbc. In relation to the seven strains now employed, it is resistant to A, B^1, B^2, C and D and susceptible to strains E and F. The gene is now known as R_3.

The results of further tests are shown in Table IV, where R_3 types are crossed with recessive, with R_1 and with R_2 types. Since both genes (R_3 and R_1) confer resistance to strain C they give a 3 : 1 ratio when

intercrossed. $R_3 \times R_2$, on the other hand, gives a 1 : 1 ratio when tested with strain E because only the R_2 gene is effective against this strain.

TABLE IV.—DERIVATIVES OF TRIPLE HYBRIDS 885(2) AND 885(3). GENE R_3

Ref. No.	Parentage		Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1929*abc*	1253*a*(12)	× A1695	C	102	156	0·65 : 1	1 : 1	$R_3 \times r$
1925*a–d*	do.	× Aquila	C	97	45	2·16 : 1	3 : 1	$R_3 \times R_1$
1926*ab*	do.	× Jakobi	C	182	72	2·53 : 1	3 : 1	$R_3 \times R_1$
1682*c*	do.	× 1318(3)	E	38	42	0·90 : 1	1 : 1	$R_3 \times R_2$
1688*d*	1270*b*(9)	× 910*a*(123)	A	70	69	1·01 : 1	1 : 1	$R_3 \times r$
1255*d*	Craigs Defiance	× 997*a*(51)	C	100	107	0·93 : 1	1 : 1	$r \times R_3$
1102*c*	885(2)	× Cardinal	C	84	26	3·23 : 1	3 : 1	$R_1R_3 \times r$
G1795	1276*b*(6)	× Aquila	C	33	10	3·30 : 1	3 : 1	$R_3 \times R_1$
G1356*b*	1276*b*(10)	× Flava	C	49	48	1·02 : 1	1 : 1	$R_3 \times r$

The results of the double test (Table V) show that where only the R_3 gene is present, the survivors of the C strain remain unaffected by strain B^2 since R_3 confers resistance to both strains and the progeny consists only of R_3 types and recessives. In the case of $R_3 \times R_1$, however, where the seedlings segregate in the ratio of approximately $1R_1R_3 : 1R_1 : 1R_3 : 1r$, the C strain kills only the recessives but the B^2 strain kills the R_1 types. The survivors (50 per cent.) consist of R_1R_3 and R_3 types.

TABLE V.—DOUBLE TEST (STRAIN C FOLLOWED BY STRAIN B^2)

Ref. No.	Parentage			Killed by C	Killed by B^2	Survived	Genotypes (Significant Terms only)
1929*c*	1253*a*(12)	× A1695	O	53	..	37	$R_3 \times r$
			E	45	..	45	
1925*cd*	do.	× Aquila	O	15	7	20	$R_3 \times R_1$
			E	10·5	10·5	21	
1926*b*	do.	× Jakobi	O	38	36	54	$R_3 \times R_1$
			E	32	32	64	
G1356*b*	1276*b*(10)	× Flava	O	48	..	49	$R_3 \times r$
			E	48·5	..	48·5	

O = observed. E = expected.

The resistant parent plants, 1253*a*(12), 1270*b*(9) and 997*a*(51), each possessing the gene R_3, were bred from triple hybrid 885(2). This triple hybrid, when crossed with Cardinal, gives a 3 : 1 ratio on testing with

strain C (Table IV), and must therefore have two genes effective against this strain. As previously shown (Black, 1945, Table I), it contains two genes conferring resistance to strain A but only one to strain B^1. One of the genes has already been identified as R_3. The other must be R_1 to meet these requirements. Incidentally all plants possessing only the R_1 gene in the original progeny would be killed off in the B^1 strain test (Black, 1945, Table I). Triple hybrid 885(2) is thus represented by R_1R_3.

A sister plant, triple hybrid 885(3), was lost at an early stage in the experiments on account of the tubers rotting in storage, and the three genes, which the original tests with strains A and B^1 revealed, could not all be identified. The surviving derivatives, *e.g.* 1276*b*(6), 1276*b*(10) and 998*a*(18), all possess only the gene R_3 (Black, 1945, Table III; 1949, Tables IV and VI).

Seedlings 1104*a*(3) and 1104*c*(2) referred to in Table VI are 2nd-generation derivatives of triple hybrid 885(4), and are resistant to strains

TABLE VI.—2ND-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4). GENES R_3 AND R_4

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1495	791*a*(116) × 1104*a*(3)	A	81	40	2·03 : 1	3 : 1	$r \times R_3R_4$
1568*b*	Epicure × 1104*c*(2)	A	123	41	3·00 : 1	3 : 1	$r \times R_3R_4$
1810*b*	30–71 × 1104*c*(2)	C	56	57	0·98 : 1	1 : 1	$r \times R_3R_4$
1563*c*	Craigs Defiance × 1104*a*(3)	E	153	159	0·96 : 1	1 : 1	
1567*b*	Epicure × do.	E	75	81	0·93 : 1	1 : 1	
1577	Majestic × do.	E	134	127	1·06 : 1	1 : 1	$r \times R_3R_4$
1583*c*	Southesk × do.	E	160	143	1·12 : 1	1 : 1	
1591*bc*	791*a*(116) × do.	E	200	182	1·10 : 1	1 : 1	
			722	692	1·04 : 1	1 : 1	
1822*a*	1104*a*(3) Selfed	E	97	46	2·11 : 1	3 : 1	R_3R_4
1564*c*	Craigs Defiance × 1104*c*(2)	E	144	152	0·95 : 1	1 : 1	
1568*a*	Epicure × do.	E	129	120	1·08 : 1	1 : 1	
1584*c*	Southesk × do.	E	195	157	1·24 : 1	1 : 1	
1803	21–4 × do.	E	88	98	0·90 : 1	1 : 1	
1808*a*	24–15 × do.	E	57	37	1·54 : 1	1 : 1	$r \times R_3R_4$
1809*a*, 1810*a*	30–71 × do.	E	126	114	1·11 : 1	1 : 1	
1812*a*	30–73 × do.	E	60	56	1·07 : 1	1 : 1	
			799	734	1·09 : 1	1 : 1	
1823*b*	1104*c*(2) Selfed	E	150	56	2·68 : 1	3 : 1	R_3R_4
1506*b*	835*a*(4) × 1104*c*(2)	E	110	118	0·93	1 : 1	$R_1 \times R_3R_4$

A, B^1, B^2, C, D and E but susceptible to strain F. In 1946 they were found to possess two genes both effective against the original B strain (now referred to as B^1), but in 1947 and 1948 the segregations obtained were typical of those resulting from the presence of a single effective gene, and it was concluded the B strain had changed in infective power between seasons 1946 and 1947 to an extent sufficient to overcome the powers of one gene (Black, 1949, Tables VII, VIII and IX). Some of the plants which proved resistant to the B^1 strain in 1946 were later attacked in the field by a new strain D. Again, in 1949 strain D appeared in the field on a proportion of the seedlings bred from 1104*a*(3) and 1104*c*(2) which had survived the tests with strain E. Samples of these plants were retained for critical test and proved to be resistant to strains A, B^1 and E and susceptible to strains B^2, C, D and F. This represents a new type of resister and the gene responsible is named R_4. Other segregates which were unaffected in the field by the D strain proved to be resistant to A, B^1, B^2, C and D and susceptible to E and F. This is the reaction of gene R_3, and consequently the constitution of 1104*a*(3) and 1104*c*(2) is represented by R_3R_4.

Additional segregations in progenies bred from 1104*a*(3) and 1104*c*(2) are contained in Table VI. Tests with strain A confirm the presence of two genes, and the tests with strains C and E respectively show that only one gene is effective in each case. In the last progeny in Table VI, obtained by crossing an R_1 type with 1104*c*(2), only R_4 types are resistant to strain E and a 1 : 1 ratio results.

The constitution of 1104*a*(3) and 1104*c*(2) is confirmed by triple tests and double tests shown in Table VII. In the triple tests the progenies were inoculated with strains A, D and E in turn, and the results are in accordance with expectation in the segregation ratio $1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain A kills the recessives (25 per cent.), strain D the R_4 types (25 per cent.), strain E the R_3 types (25 per cent.) and only the R_3R_4 types (25 per cent.) remain alive.

In the double test strain E kills the recessives and the R_3 types (50 per cent.), strain C kills the R_4 types (25 per cent.), and only the R_3R_4 types (25 per cent.) survive. When the sequence is reversed, strain C kills the recessives and the R_4 types (50 per cent.), strain E kills the R_3 types (25 per cent.), and the R_3R_4 types (25 per cent.) again survive.

Since 1104*a*(3) and 1104*c*(2) were bred from 885(4) × *S. tuberosum*, it follows that triple hybrid 885(4) must possess genes, R_3 and R_4. It was previously found, however (Black, 1945, Table I), that 885(4) had three genes conferring resistance to strain A, two of which were effective against strain B^1, and consequently one gene remains to be identified. From the

TABLE VII.—DOUBLE AND TRIPLE TESTS

Ref. No.	Parentage		Killed by A	Killed by D	Killed by E	Survived	Genotypes (Significant Terms only)
1495	791*a*(116) × 1104*a*(3)	O	40	20	31	30	r × R_3R_4
		E	30·25	30·25	30·25	30·25	
1568*b*	Epicure × 1104*c*(2)	O	41	31	44	48	r × R_3R_4
		E	41	41	41	41	
			E	C			
1567*b*	Epicure × 1104*a*(3)	O	81	39		36	r × R_3R_4
		E	78	39		39	
1568*a*	Epicure × 1104*c*(2)	O	120	67		62	r × R_3R_4
		E	124·5	62·25		62·25	
1823*b*	1104*c*(2) Selfed	O	56	40		110	R_3R_4
		E	51·5	38·625		115·875	
		T	4	3		9	
			C	E			
1810*b*	30–71 × 1104*c*(2)	O	57	25		31	r × R_3R_4
		E	56·5	28·25		28·25	

O = observed. E = expected. T = theoretical.

above information and that contained in Table VIII it will be seen that 885(4) possesses—

3 genes conferring resistance to strain A				
2 genes	,,	,,	,,	B^1
1 gene	,,	,,	,,	B^2
2 genes	,,	,,	,,	C
1 gene	,,	,,	,,	E

Genes R_3 and R_4 fulfil the requirements with respect to two genes conferring resistance to strains A and B^1, and one gene giving resistance to strains B^2, C and E. The third gene must therefore provide resistance

TABLE VIII.—DOUBLE TESTS OF PROGENIES DERIVED FROM TRIPLE HYBRID 885(4)

Ref. No.	Parentage		Killed by B^2	Killed by E	Survived	Total	Genotypes (Significant Terms only)
1464*bc*	885(4) × 910*a*(123)	O	46	26	24	96	$R_1R_3R_4$ × r
		E	48	24	24	96	
		T	4	2	2	8	
			E	C			
1819*a*	885(4) Selfed	O	9	6	61	76	$R_1R_3R_4$
		E	19	3·56	53·44	76	
		T	16	3	45	64	

O = observed. E = expected. T = theoretical.

to strains A and C, *i.e.* it must be gene R_1, and the constitution of 885(4) is therefore $R_1R_3R_4$. In critical tests 885(4) proved to be resistant to all strains except F, a behaviour which fits exactly with that expected from the genotype $R_1R_3R_4$.

One of the triple hybrids, viz. 886(1), proved to be resistant to all strains except C. This plant produced, on crossing with a recessive, a family of 27 seedlings, of which 20 were resistant and 7 susceptible to strain A. This is a close approximation to a 3 : 1 ratio and indicates the presence of two genes. Since 886(1) is susceptible to C only, the two genes would appear to be R_2 and R_4. In order to confirm this constitution, the 20 seedlings which survived the A strain test were inoculated with strain B^2. Six of them proved to be susceptible. The remaining 14 plants were inoculated with strain C and, as expected, all proved to be susceptible. The genotype of 886(1) is therefore R_2R_4, and the segregation ratio $1R_2R_4 : 1R_2 : 1R_4 : 1r$ in which the A strain kills the recessives and the B^2 strain the R_4 types.

Originally the F_1 hybrid, 735, was believed to have four genes conferring resistance to strain A (Black, 1945, Table I). It has proved to be resistant to all strains, and four genes have now been identified in the material bred from it. Only two genes, R_1 and R_3, give resistance to strain C, and consequently a selfed progeny of 735 tested with strain C should segregate in the ratio of 15 resistants : 1 susceptible. Such a ratio was obtained (Table IX).

TABLE IX.—PROGENY OF F_1 HYBRID 735 TESTED WITH STRAIN C

Ref. No.	Parentage	Number of Seedlings		Ratio		Genotypes (Significant Terms only)
		R	r	Observed	Expected	
1109	735 Selfed	59	4	14·75 : 1	15 : 1	$R_1R_2R_3R_4$

The F_1 hybrid may therefore be credited with the genes R_1, R_2, R_3 and R_4, and *S. demissum* (CPC 2127) with the same genes in the homozygous condition. No indication has yet been observed of the presence of others.

A number of offspring of 1104*a*(3) and 1104*c*(2) which were resistant to all strains except F were used as female parents in crosses with recessives and with Aquila (gene R_1). The constitution of the female parents is the same throughout (R_3R_4), as shown in Table X where the C strain was employed for test purposes. In crosses with recessive pollen parents only the R_3 gene is effective and segregations of approximately 1 : 1 are

obtained. In crosses with Aquila, however, in which gene R_1 is also effective, the ratios obtained approximate 3 : 1.

TABLE X.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) TESTED WITH STRAIN C

Ref. No.	Parentage	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1964*a*	1564*a*(9) × Sickingen	87	106	0·82 : 1	1 : 1	$R_3R_4 \times r$
1965*a*	do. × 910*a*(123)	62	68	0·91 : 1	1 : 1	
1970*ab*	1567*a*(7) × 11–79	166	158	1·05 : 1	1 : 1	
1976*abc*	1591*a*(19) × 11–79	155	217	0·71 : 1	1 : 1	
		470	549	0·86 : 1	1 : 1	
1933*ab*	1488*b*(1) × Aquila	32	12	2·67 : 1	3 : 1	$R_3R_4 \times R_1$
1967	1564*a*(12) × do.	49	15	3·27 : 1	3 : 1	
1971*bc*	1584*b*(7) × do.	116	37	3·14 : 1	3 : 1	
1974*abc*	1591*a*(19) × do.	46	24	1·92 : 1	3 : 1	
		243	88	2·76 : 1	3 : 1	

Similar progenies were employed in a double test (Table XI), in which strain C was followed by strain E. Where a recessive was used as pollen parent the segregation ratio is $1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain C kills the recessives and the R_4 types (50 per cent.), strain E kills the R_3 types, and the R_3R_4 types survive. With Aquila as pollen parent, however, the ratio

TABLE XI.—DOUBLE TESTS

Ref. No.	Parentage		Killed by C	Killed by E	Survived	Genotypes (Significant Terms only)
1964*a*	1564*a*(9) × Sickingen	O	106	31	56	$R_3R_4 \times r$
		E	96·5	48·25	48·25	
1965*a*	do. × 910*a*(123)	O	68	33	29	
		E	65	32·5	32·5	
1970*ab*	1567*a*(7) × 11–79	O	158	75	91	
		E	162	81	81	
1976*ab*	1591*a*(19) × do.	O	159	44	63	
		E	133	66·5	66·5	
1933*ab*	1488*b*(1) × Aquila	O	12	19	13	$R_3R_4 \times R_1$
		E	11	16·5	16·5	
1967	1564*a*(12) × do.	O	15	29	20	
		E	16	24	24	
1971*bc*	1584*b*(7) × do.	O	37	52	64	
		E	38·25	57·375	57·375	
			C	B^2		
1976*c*	1591*a*(19) × 11–79	O	58	..	48	$R_3R_4 \times r$
		E	53	..	53	
1974*abc*	1591*a*(19) × Aquila	O	24	12	34	$R_3R_4 \times R_1$
		E	17·5	17·5	35	

O = observed. E = expected.

is $1R_1R_3R_4 : 1R_3R_4 : 1R_1R_3 : 1R_3 : 1R_1R_4 : 1R_4 : 1R_1 : 1r$. Strain C kills the recessive and R_4 types (25 per cent.), strain E kills the R_1, R_3 and R_1R_3 types (37·5 per cent.), and the remainder (37·5 per cent.) survive.

When strain C is followed by strain B^2, the latter has no effect on the C resisters in progenies derived from a recessive pollen parent, due to the presence of the R_3 gene. Where Aquila is pollen parent, however, strain C kills the recessive and the R_4 types (25 per cent.), strain B^2 kills the R_1 and R_1R_4 types (25 per cent.), and the $R_1R_3R_4$, R_3R_4, R_1R_3 and R_3 types (50 per cent.) survive.

Several seedlings bred from 1104*a*(3) and 1104*c*(2) crossed with recessives were used as female parents in crosses with 1318(3) (gene R_2) and the segregations are shown in Table XII. Seedlings 1563*a*(5) and 1563*a*(6) were susceptible to strain E, due to the absence of gene R_4, while seedlings 1563*b*(8) and 1564*a*(9) were resistant to all strains except F due to the presence of both genes R_3 and R_4. The segregations obtained in relation to the strains employed are in accordance with expectations.

TABLE XII.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) CROSSED WITH R_2 TYPE

Ref. No.	Parentage	Strain	Number of Seedlings		Ratio		Genotypes (Significant Terms only)
			R	r	Observed	Theoretical	
1959*a*	1563*a*(5) × 1318(3)	E	46	56	0·82 : 1	1 : 1	$R_3 \times R_2$
1960*ab*	1563*a*(6) × do.	B^2	117	32	3·66 : 1	3 : 1	$R_3 \times R_2$
1962*a*	1563*b*(8) × do.	E	82	30	2·73 : 1	3 : 1	$R_3R_4 \times R_2$
1966*a–d*	1564*a*(9) × do.	C	182	225	0·81 : 1	1 : 1	$R_3R_4 \times R_2$

Similar progenies were submitted to double and triple tests and the results are shown in Table XIII. The progenies derived from $R_3R_4 \times R_2$ segregate according to the ratio $1R_2R_3R_4 : 1R_2R_3 : 1R_2R_4 : 1R_2 : 1R_3R_4 : 1R_3 : 1R_4 : 1r$. Strain C kills the recessives, R_2, R_4 and R_2R_4 types (50 per cent.), strain E kills the R_3 types (12·5 per cent.), and the remainder (37·5 per cent.) survive. When strain F is used instead of E for the second part of the test, it kills the R_3 and R_3R_4 types (25 per cent.) and only 25 per cent. survive.

The segregation in the progenies derived from $R_3 \times R_2$ is represented by the ratio $1R_2R_3 : 1R_2 : 1R_3 : 1r$. The E strain kills the recessives and R_3 types (50 per cent.), the F strain is ineffective against the remainder, but the C strain kills the R_2 types (25 per cent.) and only the R_2R_3 types (25 per cent.) survive. In the last case strain B^2 kills the recessives (25 per cent.), F kills the R_3 types (25 per cent.), C kills the R_2 types (25 per cent.), and again the only survivors are the R_2R_3 types (25 per cent.).

TABLE XIII.—DOUBLE AND TRIPLE TESTS

Ref. No.	Parentage		Killed by C	Killed by E	Killed by F	Survived	Genotypes (Significant Terms only)
1966*a*	1564*a*(9) × 1318(3)	O	76	13		51	$R_3R_4 \times R_2$
		E	70	17·5		52·5	
			C	F			
1966*b*	1564*a*(9) × 1318(3)	O	72	30		25	$R_3R_4 \times R_2$
		E	63·5	31·75		31·75	
			E	F	C		
1959*a*	1563*a*(5) × 1318(3)	O	56	..	21	25	$R_3 \times R_2$
		E	51	..	25·5	25·5	
			B^2	F	C		
1960*ab*	1563*a*(6) × 1318(3)	O	32	35	39	43	$R_3 \times R_2$
		E	37·25	37·25	37·25	37·25	

O = observed. E = expected.

Two seedlings, 1306*a*(2) and 1306*a*(15), obtained by selfing 1104*a*(3) (Black 1945, Table IV), were employed as parents in crosses with recessive types and the results are shown in Table XIV. Various progenies bred from 1306*a*(2) were previously examined in A and B^2 strain tests (Black, 1949, Tables X and XII), and the results indicated that two genes were in

TABLE XIV.—3RD- AND 4TH-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) (1306*a*(2), 1306*a*(15) AND 1439*a*(4))

Ref. No.	Parentage		Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1574*a*	Gladstone	× 1306*a*(2)	B^2+C	34	43	0·79 : 1	1 : 1	$r \times R_3R_4$
1610*b*	1–106	× do.	E	65	70	0·93 : 1	1 : 1	
1431*a*	Arran Victory	× 1306*a*(15)	B^1	108	17	6·35 : 1	7 : 1	$r \times R_3R_3R_4$
1433*abc*	Craigs Defiance	× do.	B^1	354	37	9·57 : 1	7 : 1	
1434*a*	do.	× do.	B^1	75	10	7·50 : 1	7 : 1	
1436	Gladstone	× do.	B^1	141	9	15·67 : 1	7 : 1	
1437*abc*	Majestic	× do.	B^1	406	52	7·81 : 1	7 : 1	
1438	Southesk	× do.	B^1	177	12	14·75 : 1	7 : 1	
1439*ab*	do.	× do.	B^1	178	23	7·74 : 1	7 : 1	
				1439	160	8·99 : 1	7 : 1	
1799	1439*a*(4)	× Flava	C	95	99	0·96 : 1	1 : 1	$R_3 \times r$
1800*a*	do.	× 834*c*(29)	C	80	41	1·95 : 1	3 : 1	$R_3 \times R_1$

operation. From these facts and the evidence set out in Tables XIV and XV it is apparent that 1306*a*(2) possesses—

2 genes conferring resistance to strain A
1 gene ,, ,, ,, B^2
1 ,, ,, ,, ,, C
1 ,, ,, ,, ,, E

The genes may thus be identified as R_3R_4, the same constitution as 1104*a*(3) from which 1306*a*(2) was bred.

The segregations obtained from 1306*a*(15), although slightly inconsistent, are characterised by an unexpectedly high proportion of resistant plants (Table XIV). The average in tests with strain B^1 shows a ratio of 8·99 : 1, but if this be regarded as a theoretical 7 : 1 ratio, then the constitution of 1306*a*(15) may be deduced from the results of the double tests shown in Table XV. The available information indicates that 1306*a*(15) possesses—

3 genes conferring resistance to strain A
3 ,, ,, ,, ,, B^1
2 ,, ,, ,, ,, B^2
2 ,, ,, ,, ,, C
1 gene ,, ,, ,, E

Since it was bred from 1104*a*(3) only R_3 and R_4 genes can be present, and the constitution $R_3R_3R_4$ is the only one which fits. Such a genotype might be expected to exhibit some irregularity in segregations because of the presence of two R_3 genes and the relative affinity of the chromosomes carrying them. Consistent pairing of these homologues would of course

TABLE XV.—DOUBLE AND QUADRUPLE TESTS

Ref. No.	Parentage		Killed by A	C	B^2	E	Survived	Total	Genotypes (Significant Terms only)
1824*b*	1306*a*(2) Selfed	O	10	22	..	23	53	108	R_3R_4
		E	6·75	20·25	..	20·25	60·75	108	
		T	1	3	..	3	9	16	
			A		B^2				
1433*d*	Craigs Defiance × 1306*a*(15)	O	11		6		65	82	r × $R_3R_3R_4$
		E	10·25		10·25		61·5	82	
		T	1		1		6	8	
				C		E			
1431*b*	Arran Victory × 1306*a*(15)	O		23		54	40	117	r × $R_3R_3R_4$
		E		29·25		43·875	43·875	117	
		T		2		3	3	8	

O = observed. E = expected. T = theoretical.

produce only resistant offspring, but a relatively greater affinity at meiosis would merely tend to increase the proportion of resistant seedlings and give ratios such as those observed in Tables XIV and XV.

A seedling, 1439*a*(4), bred from Southesk × 1306*a*(15) was crossed with a recessive and an R_1 type and gave 1 : 1 and 3 : 1 ratios respectively when tested with strain C (Table XIV). Since 1439*a*(4) is susceptible to strain E, the R_4 gene must be absent and its constitution is accordingly represented by R_3.

Another seedling, 1307*a*(23), which was obtained by selfing 1104*a*(16) (Black, 1945, Table IV), also gave abnormal segregation ratios. It was found to be resistant to strains A, B^1, B^2, C and D and susceptible to E and F, a series of reactions typical of those of R_3 plants. Since the parent plant 1104*a*(16) had only one gene, the offspring 1307*a*(23) may be represented by R_3R_3.

In Table XVI progeny tests of 1307*a*(23) are set out in three groups, viz. recessive × 1307*a*(23), R_3 types × 1307*a*(23) and 1307*a*(23) selfed. The R_3 types in the second group were members of progenies previously examined (Black, 1945, Tables II and III). The outstanding feature of all progenies is the large and consistent excess of resistant segregates compared with the theoretical ratios. Since 1307*a*(23) can have inherited not more than two genes, it is concluded that the high proportion of

TABLE XVI.—3RD-GENERATION DERIVATIVES OF TRIPLE HYBRID 885(4) (1307*a*(23))

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1566*a*	Craigs Defiance × 1307*a*(23)	B^2	117	16	7·31 : 1	3 : 1	
1566*bc*	do. × do.	C	141	15	9·40 : 1	3 : 1	
1570*ab*	Epicure × do.	B^2	78	13	6·00 : 1	3 : 1	r × R_3R_3
1575	Gladstone × do.	B^2	175	20	8·75 : 1	3 : 1	
1593*ab*	791*a*(116) × do.	B^2	222	30	7·40 : 1	3 : 1	
			733	94	7·80 : 1	3 : 1	
1599*ab*	1253*a*(15) × 1307*a*(23)	B^2	96	6	16·00 : 1	7 : 1	
1602*ab*	1256*a*(23) × do.	B^2	212	13	16·31 : 1	7 : 1	$R_3 \times R_3R_3$
1606	1258*a*(19) × do.	B^2	64	10	6·40 : 1	7 : 1	
			372	29	12·83 : 1	7 : 1	
1631*ab*	1307*a*(23) Selfed	A	146	5	29·20 : 1	15 : 1	
1527*abc*	do.	B^1	231	10	23·10 : 1	15 : 1	R_3R_3
1631*c*, 1726*bc*	do.	B^2	200	5	40·00 : 1	15 : 1	
			577	20	28·85 : 1	15 : 1	

resistant seedlings observed is due to a greater affinity of the R_3-bearing chromosomes for each other than for their alternative allelomorphs which probably had different specific origin. The figures indicate that the chromosomes carrying the R_3 genes paired with each other almost as frequently as they did with the alternative allelomorphs which would be their normal partners if allo-syndesis prevailed. Apparently auto-syndesis and allo-syndesis occurred in approximately equal proportions in this tetraploid plant.

Seedling 882(5) *and Derivatives*

Seedling 882(5), which has been widely employed as a female parent in breeding experiments, was bred from the original *S. demissum–S. tuberosum* material and its pedigree is detailed in fig. 4. Although *S. Rybinii* also features in the pedigree, its employment as a parent was in this case not directly associated with *S. demissum* and may be regarded as incidental. The blight resistance of seedling 882(5) was inherited from 692*a*(52), a selection from family 692 (Black, 1943, Table VI).

It was shown in earlier tests (Black, 1949, Tables XI and XII) that 882(5) possessed two genes for resistance. This information, together with that set out in Tables XVII and XVIII dealing with 882(5) crossed with recessives, demonstrates that 882(5) possesses—

2 genes	conferring	resistance	to strain	A
1 gene	,,	,,	,,	B^2
1 ,,	,,	,,	,,	C
1 ,,	,,	,,	,,	E
1 ,,	,,	,,	,,	F

The genes present must therefore be R_1R_2.

When R_1R_2 types are crossed with recessives the genotypic segregation is $1R_1R_2 : 1R_1 : 1R_2 : 1r$. The A strain can kill only the recessives and a 3 : 1 ratio results. Strain C kills the R_2 types as well as the recessives, giving a 1 : 1 ratio, while strain E kills the R_1 types and the recessives, giving also a 1 : 1 ratio.

In the double tests (Table XVIII) strain C kills the R_2 types and the recessives (50 per cent.), strain F kills the R_1 types (25 per cent.), and the R_1R_2 types survive (25 per cent.). When strain E is substituted for F the same results are obtained. If the sequence is reversed, strain E followed by C, the recessives and R_1 types are killed by E, the R_2 types by C, and the R_1R_2 types survive as before.

TABLE XVII.—5TH GENERATION DERIVATIVES OF *S. demissum* × *S. tuberosum* (882(5))

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1508*b*, 1509*ab*	882(5) × Katahdin	A	271	98	2·77 : 1	3 : 1	$R_1R_2 \times r$
1511*b*	882(5) × M233(13)	C	64	58	1·10 : 1	1 : 1	
1914*a*	do. × Alness	C	58	85	0·68 : 1	1 : 1	
1915*ab*	do. × Gladstone	C	91	93	0·98 : 1	1 : 1	
1916*a*	do. × Sickingen	C	75	68	1·10 : 1	1 : 1	$R_1R_2 \times r$
1921*ab*	do. × 21–4	C	131	129	1·01 : 1	1 : 1	
1922*a*	do. × 23–22	C	43	37	1·16 : 1	1 : 1	
1923*a–j*	do. × 11–79	C	845	754	1·12 : 1	1 : 1	
			1307	1224	1·07 : 1	1 : 1	
1670*bd*	882(5) × 910*a*(123)	E	75	63	1·19 : 1	1 : 1	
1790*ab*	do. × Sickingen	E	99	96	1·03 : 1	1 : 1	$R_1R_2 \times r$
1791	do. × 21–4	E	46	54	0·85 : 1	1 : 1	
1792*ab*	do. × 23–22	E	82	86	0·95 : 1	1 : 1	
			302	299	1·01 : 1	1 : 1	

TABLE XVIII.—DOUBLE TESTS

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Genotypes (Significant Terms only)
1915*b*	882(5) × Gladstone	O	38	23	19	$R_1R_2 \times r$
		E	40	20	20	
1921*a*	do. × 21–4	O	57	37	41	$R_1R_2 \times r$
		E	67·5	33·75	33·75	
1922*a*	do. × 23–22	O	37	20	23	$R_1R_2 \times r$
		E	40	20	20	
1923*b–d*, *g–j*	do. × 11–79	O	506	290	289	$R_1R_2 \times r$
		E	542·5	271·25	271·25	
			C	E		
1923*a*	882(5) × 11–79	O	82	44	51	$R_1R_2 \times r$
		E	88·5	44·25	44·25	
			E	C		
1670*bd*	882(5) × 910*a*(123)	O	63	30	45	$R_1R_2 \times r$
		E	69	34·5	34·5	

O = observed. E = expected.

882(5) was crossed with R_1 types (bred from multiple hybrid W800(2)) and R_2 types (related to *S. demissum–S. tuberosum* hybrid 877*a*(34)), and the results are shown in Tables XIX and XX. In seedlings bred

from $R_1R_2 \times R_1$, the R_2 gene only is effective against strain E and a 1 : 1 ratio results. Progenies obtained from $R_1R_2 \times R_2$ have two genes effective against strains B^2 and E and give 3 : 1 ratios, but only one gene is effective against C and 1 : 1 ratios result.

TABLE XIX.—PROGENIES DERIVED FROM 882(5) CROSSED WITH R_1 AND R_2 TYPES

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1664*abc*	882(5) × 834*b*(6)	E	220	214	1·03 : 1	1 : 1	$R_1R_2 \times R_1$
1514*b*	do. × 834*c*(29)	E	78	86	0·91 : 1	1 : 1	
1668*abc*	do. × do.	E	206	226	0·91 : 1	1 : 1	
			504	526	0·96 : 1	1 : 1	
1671	882(5) × 1318(3)	B^2	167	55	3·04 : 1	3 : 1	$R_1R_2 \times R_2$
1672*a*							
1673*c*	882(5) × 1318(3)	C	46	46	1·00 : 1	1 : 1	$R_1R_2 \times R_2$
1972*b*	do. × do.	C	54	52	1·04 : 1	1 : 1	
1917*ab*	do. × 877*a*(34)	C	54	42	1·29 : 1	1 : 1	
			154	140	1·10 : 1	1 : 1	
1673*ab*	882(5) × 1318(3)	E	173	58	2·98 : 1	3 : 1	$R_1R_2 \times R_2$

TABLE XX.—DOUBLE TESTS

Ref. No.	Parentage		Killed by E	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1664*b*	882(5) × 834*b*(6)	O	63	17	45	125	$R_1R_2 \times R_1$
		E	62·5	15·625	46·875	125	
		T	4	1	3	8	
1668*c*	do. × 834*c*(29)	O	79	22	40	141	$R_1R_2 \times R_1$
		E	70·5	17·625	52·875	141	
		T	4	1	3	8	
			B^2	C			
1671	882(5) × 1318(3)	O	20	24	45	89	$R_1R_2 \times R_2$
		E	22·25	33·375	33·375	89	
		T	2	3	3	8	
			C	F			
1917*ab*	882(5) × 877*a*(34)	O	42	13	41	96	$R_1R_2 \times R_2$
		E	48	12	36	96	
		T	4	1	3	8	

O = observed. E = expected. T = theoretical.

R_1R_2 types × R_1 types segregate according to the genotypic ratio $1R_1R_1R_2 : 2R_1R_2 : 1R_2 : 1R_1R_1 : 2R_1 : 1r$. As shown in double tests (Table XX), the E strain kills 50 per cent., *i.e.* all segregates lacking R_2;

of the remainder the C strain kills 12·5 per cent., *i.e.* those lacking R_1. The survivors, 37·5 per cent., have both genes in their constitution.

In the progenies obtained from $R_1R_2 \times R_2$ the genotypic ratio is $1R_1R_2R_2 : 2R_1R_2 : 1R_1 : 1R_2R_2 : 2R_2 : 1r$. The B^2 strain kills 25 per cent., *i.e.* those lacking R_2, the C strain a further 37·5 per cent., *i.e.* those lacking R_1, and the survivors, 37·5 per cent., possess both genes. In the last progeny mentioned in Table XX the C strain kills those lacking R_1 (50 per cent.), the F strain kills those lacking R_2 (a further 12·5 per cent.), and again the plants possessing both genes survive (37·5 per cent.).

Parent plants 1517*b*(2) and 1509*a*(4) (Table XXI) bred from 882(5) × recessive were back-crossed to recessives. The results show that 1517*b*(2) has the same constitution as 882(5), viz. R_1R_2, and that the ratios obtained are in close agreement with those calculated on the basis of the genotypic ratio $1R_1R_2 : 1R_1 : 1R_2 : 1r$.

TABLE XXI.—DOUBLE TESTS OF PROGENIES DERIVED FROM (882(5) × RECESSIVE) × RECESSIVE

Ref. No.	Parentage		Killed by C	Killed by E	Survived	Genotypes (Significant Terms only)
1951*a*	1517*b*(2) × 910*a*(123)	O	75	39	41	$R_1R_2 \times r$
		E	77·5	38·75	38·75	
1952*a*	do. × 23–22	O	59	22	29	$R_1R_2 \times r$
		E	55	27·5	27·5	
			C	F		
1951*b*	1517*b*(2) × 910*a*(123)	O	23	23	17	$R_1R_2 \times r$
		E	31·5	15·75	15·75	
1952*bcd*	do. × 23–22	O	206	117	103	$R_1R_2 \times r$
		E	213	106·5	106·5	
			F	C		
1940*a*	1509*a*(4) × 23–22	O	65	75	..	$R_2 \times r$
		E	70	70	..	

O = observed. E = expected.

In the case of 1509*a*(4), the F strain killed half of the progeny and the C strain killed the remainder. Obviously gene R_1 is absent from this plant and its constitution must be represented by R_2.

In Table XXII the parent plants 1508*b*(3), 1509*a*(3), 1517*a*(1) and 1517*b*(2), bred from 882(5) × recessive, were crossed with R_1 and R_3 types. 1517*b*(2) proved resistant to all strains, but the others were susceptible to strain C. The segregations observed show that 1508*b*(3), 1509*a*(3) and 1517*a*(1) are R_2 types and that 1517*b*(2) is represented by R_1R_2. In family

TABLE XXII.—PROGENIES DERIVED FROM (882(5) × RECESSIVE) × R_1 AND R_2 TYPES

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1898*ab*	835*a*(4) × 1508*b*(3)	C	76	105	0·72 : 1	1 : 1	$R_1 \times R_2$
1930*bc*	1439*a*(4) × 1508*b*(3)	C	111	123	0·90 : 1	1 : 1	$R_3 \times R_2$
1930*d*	do. × do.	F	41	39	1·05 : 1	1 : 1	
1899*acg*	853*a*(4) × 1509*a*(3)	C	187	209	0·89 : 1	1 : 1	$R_1 \times R_2$
1899*be*	do. × do.	F	118	142	0·83 : 1	1 : 1	
1943*a–k*	1517*a*(1) × Aquila	C	411	480	0·86 : 1	1 : 1	$R_2 \times R_1$
1944	do. × 914*a*(91)	C	49	59	0·83 : 1	1 : 1	
1948*a–g*, 1949*bcdj*	1517*b*(2) × Aquila	C	1365	464	2·94 : 1	3 : 1	$R_1R_2 \times R_1$
1949*ae*	do. × do.	F	165	159	1·04 : 1	1 : 1	
1949*f*	do. × do	C+F	84	92	4·57 : 5	3 : 5	
1950*ab*	do. × 834*c*(29)	C	73	29	2·52 : 1	3 : 1	

TABLE XXIII.—DOUBLE TESTS

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Total	Genotypes (Significant Terms only)
1898*ab*	835*a*(4) × 1508*b*(3)	O	105	41	35	181	$R_1 \times R_2$
		E	90·5	45·25	45·25	181	
1930*bc*	1439*a*(4) × do.	O	123	57	54	234	$R_3 \times R_2$
		E	117	58·5	58·5	234	
1899*ac*	835*a*(4) × 1509*a*(3)	O	134	66	62	262	$R_1 \times R_2$
		E	131	65·5	65·5	262	
1943*c–k*	1517*a*(1) × Aquila	O	325	128	137	590	$R_2 \times R_1$
		E	295	147·5	147·5	590	
1944	do. × 914*a*(91)	O	59	25	24	108	$R_2 \times R_1$
		E	54	27	27	108	
1948*cdfg*, 1949*bc*	1517*b*(2) × Aquila	O	225	361	345	931	$R_1R_2 \times R_1$
		E	232·75	349·125	349·125	931	
		T	2	3	3	8	
1950*ab*	do. × 834*c*(29)	O	29	30	43	102	$R_1R_2 \times R_1$
		E	25·5	38·25	38·25	102	
		T	2	3	3	8	
			F	C			
1930*d*	1439*a*(4) × 1508*b*(3)	O	39	22	19	80	$R_3 \times R_2$
		E	40	20	20	80	
1899*b*	835*a*(4) × 1509*a*(3)	O	58	29	23	110	$R_1 \times R_2$
		E	55	27·5	27·5	110	
1949*ae*	1517*b*(2) × Aquila	O	159	46	119	324	$R_1R_2 \times R_1$
		E	162	40·5	121·5	324	
		T	4	1	3	8	
			C	B^2			
1949*d*	1517*b*(2) × Aquila	O	51	66	83	200	$R_1R_2 \times R_1$
		E	50	75	75	200	
		T	2	3	3	8	
			C	E			
1948*a*	1517*b*(2) × Aquila	O	41	67	72	180	$R_1R_2 \times R_1$
		E	45	67·5	67·5	180	
		T	2	3	3	8	

O = observed. E = expected. T = theoretical.

1949*f* a mixture of C and F strains were employed and the resulting segregation approached the theoretical 3 : 5 ratio.

The same or similar progenies were subjected to double tests as shown in Table XXIII. In crosses between R_1 types and R_2 types the C strain kills the recessives and the R_2 plants (50 per cent.), the F strain kills the R_1 plants (25 per cent.), and the R_1R_2 types (25 per cent.) survive. The same figures are obtained in $R_3 \times R_2$ progenies because strains C and F have the same effect on R_3 as on R_1 genotypes. Where R_1R_2 types are crossed with R_1, the C strain kills the recessives and R_2 types (25 per cent.), the F strain kills the R_1 types (37·5 per cent.), and the survivors (37·5 per cent.) are those possessing both genes. When the sequence is reversed (F followed by C), the proportions killed in $R_1 \times R_2$ families are the same as before, but in progenies obtained from $R_1R_2 \times R_1$ the F strain kills 50 per cent., the C strain 12·5 per cent., and the same 37·5 per cent. survive. Table XXIII also shows that if B^2 or E is substituted for F, the results remain exactly the same since B^2, E and F have the same effect on R_1 and on R_2 genotypes.

Seedling 1512*c*(14), bred from 882(5) $(R_1R_2) \times R_1$ type (Black, 1949, Table XI), was used as a pollen parent in a series of crosses (Table XXIV). Since it proved to be susceptible to strain C and resistant to all the others, it must possess only the gene R_2. That this is so is confirmed by the results of crosses with recessives, R_1, R_3 and R_3R_4 types shown in Table XXIV, and also by the results of the double and triple tests contained in

TABLE XXIV.—PROGENIES DERIVED FROM 1512*c*(14) (882(5) × R_1 TYPE) CROSSED WITH RECESSIVE, R_1, R_3 and R_3R_4 TYPES

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1912*a*	Ulster Supreme × 1512*c*(14)	F	81	77	1·05 : 1	1 : 1	$r \times R_2$
1977*a*	24–15 × do.	E	100	90	1·11 : 1	1 : 1	
1900*bde*	835*a*(4) × 1512*c*(14)	C	155	192	0·81 : 1	1 : 1	$R_1 \times R_2$
1905*a*	Kennebec × do.	C	43	53	0·81 : 1	1 : 1	
1924*abc*	914*a*(12) × do.	C	193	205	0·94 : 1	1 : 1	
			391	450	0·87 : 1	1 : 1	
1900*f*	835*a*(4) × 1512*c*(14)	C+F	39	108	1·08 : 3	1 : 3	$R_1 \times R_2$
1928*abe*	1253*a*(12) × 1512*c*(14)	C	164	174	0·94 : 1	1 : 1	$R_3 \times R_2$
1928*fh*	do. × do.	F	111	114	0·97 : 1	1 : 1	
1931*abk*	1439*a*(4) × do.	C	380	401	0·95 : 1	1 : 1	
1934*a–d*	1488*b*(1) × 1512*c*(14)	C	215	225	0·96 : 1	1 : 1	$R_3R_4 \times R_2$
1980*a*	1512*c*(14) Selfed	E	114	38	3·00 : 1	3 : 1	R_2

Table XXV. Its practical value in crosses with recessives is doubtful, but in crosses with R_1, R_3 or R_3R_4 types, 25 per cent. of the seedlings in each case are resistant to all seven strains. $R_1 \times R_2$ gives the segregation ratio $1R_1R_2 : 1R_1 : 1R_2 : 1r$ in which only the R_1R_2 types can survive the

TABLE XXV.—DOUBLE AND TRIPLE TESTS

Ref. No.	Parentage		Killed by E	F	C	Survived	Genotypes (Significant Terms only)
1977*a*	24–15 × 1512*c*(14)	O	90	..	100	..	$r \times R_2$
		E	95	..	95	..	
			C	B^2	F		
1900*e*	835*a*(4) × 1512*c*(14)	O	44	22	..	24	$R_1 \times R_2$
		E	45	22·5	..	22·5	
			C	B^2			
1924*c*	914*a*(12) × 1512*c*(14)	O	64	37		34	$R_1 \times R_2$
		E	67·5	33·75		33·75	
1928*e*	1253*a*(12) × 1512*c*(14)	O	69	..		67	$R_3 \times R_2$
		E	68	..		68	
			C	E			
1934*a*	1488*b*(1) × 1512*c*(14)	O	73	21		51	$R_3R_4 \times R_2$
		E	72·5	18·125		54·375	
		T	4	1		3	
			C	F			
1905*a*	Kennebec × 1512*c*(14)	O	53	24		19	$R_1 \times R_2$
		E	48	24		24	
1924*ab*	914*a*(12) × 1512*c*(14)	O	141	68		54	$R_1 \times R_2$
		E	131·5	65·75		65·75	
1928*b*	1253*a*(12) × 1512*c*(14)	O	64	25		33	$R_3 \times R_2$
		E	61	30·5		30·5	
1931*ab*	1439*a*(4) × 1512*c*(14)	O	306	144		145	$R_3 \times R_2$
		E	297·5	148·75		148·75	
1934*bcd*	1488*b*(1) × 1512*c*(14)	O	152	79		64	$R_3R_4 \times R_2$
		E	147·5	73·75		73·75	
		T	4	2		2	
			F	C			
1928*f*	1253*a*(12) × 1512*c*(14)	O	47	24		25	$R_3 \times R_2$
		E	48	24		24	

O = observed. E = expected. T = theoretical.

double test of strain C with either B^2, or E or F. In the case of $R_3 \times R_2$ the segregation ratio is $1R_2R_3 : 1R_2 : 1R_3 : 1r$, and strain C together with E or F kill all except the R_2R_3 types. If strain B^2 is used instead of E or F, the R_3 types also survive. $R_3R_4 \times R_2$ gives the segregation ratio $1R_2R_3R_4 :$

$1R_2R_3 : 1R_2R_4 : 1R_2 : 1R_3R_4 : 1R_3 : 1R_4 : 1r$. If strains C and E are used the survivors are the $R_2R_3R_4$, R_2R_3 and R_3R_4 types (37·5 per cent.), but if E is replaced by F the R_3R_4 type is also killed, and the proportion of survivors is reduced to 25 per cent.

A plant of similar origin, 1512*d*(4), proved to be resistant to all seven strains, and when crossed with recessives the progenies segregated in the proportion of 7·2 resistants : 1 susceptible using strain C (Table XXVI). Had it inherited the dominant genes of both parents, $R_1R_2 \times R_1$, then a 3 : 1

TABLE XXVI.—PROGENIES DERIVED FROM 1512*d*(4) AND 1514*a*(1) (882(5) × R_1 TYPE) CROSSED WITH RECESSIVE AND R_1R_2 TYPES

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1896	Bintje × 1512*d*(4)	C	17	1	17·00 : 1	3 : 1	r × $R_1R_1R_2$
1903*ab*	International Kidney × 1512*d*(4)	C	72	8	9·00 : 1	3 : 1	
1908*abc*	King Edward VII × 1512*d*(4)	C	91	16	5·69 : 1	3 : 1	
			180	25	7·20 : 1	3 : 1	
1913*a–e*	Up-to-Date × 1514*a*(1)	C	145	217	0·67 : 1	1 : 1	r × R_1R_2
1918*a*	882(5) × do.	C	89	39	2·28 : 1	3 : 1	$R_1R_2 \times R_1R_2$
1918*b*	do. × do.	F	66	26	2·54 : 1	3 : 1	
1981*ac*	1514*a*(1) Selfed	F	321	106	3·03 : 1	3 : 1	R_1R_2

ratio would be expected provided the two R_1 genes remained independent from each other. The segregations indicate, however, that the chromosomes carrying the R_1 genes paired, and that the frequency of pairing was even greater than that normally occurring in an autotetraploid (5 : 1). Apparently the affinity between the two chromosomes concerned was greater for each other than for the corresponding chromosomes lacking R_1 genes, since the frequency of pairing was about 50 per cent. Had their affinity been absolute, one R_1 gene would have been inherited by every plant, as in the case of a homozygous diploid, and all would have been resistant to strain C. Both auto-syndesis and allo-syndesis therefore occurred in 1512*d*(4), as in 1306*a*(15) and 1307*a*(23) already discussed.

In the double test (Table XXVII) the deficiency of C susceptibles is more or less equally divided between the C resistant–F susceptible segregates and the CF resistants, suggesting that half of the expected recessives and R_2 types had inherited gene R_1. If so, then the number of plants in the progeny possessing both R_1 genes will be correspondingly less. On the basis of 50 per cent. pairing of chromosomes carrying R_1

genes, the segregation would be such that in a theoretical progeny of 16, strain C would kill 2, strain F would kill 7, and 7 would survive. The observed ratios closely approximate these figures.

TABLE XXVII.—DOUBLE TESTS

Ref. No.	Parentage		Killed by C	Killed by F	Survived	Total	Genotypes (Significant Terms only)
1896	Bintje × 1512*d*(4)		1	10	7	18	$r \times R_1R_1R_2$
1903*ab*	International Kidney × 1512*d*(4)		8	36	36	80	
1908*bc*	King Edward VII × 1512*d*(4)		7	28	27	62	
		O	16	74	70	160	
		E	40	60	60	160	
		T	2	3	3	8	
			C	F			
1913*ab*	Up-to-Date × 1514*a*(1)	O	83	22	27	132	$r \times R_1R_2$
		E	66	33	33	132	
		T	2	1	1	4	
1918*a*	882(5) × do.	O	39	27	62	128	$R_1R_2 \times R_1R_2$
		E	32	24	72	128	
		T	4	3	9	16	
			F	C			
1918*b*	do. × do.	O	26	22	44	92	$R_1R_2 \times R_1R_2$
		E	23	17·25	51·75	92	
		T	4	3	9	16	

O = observed. E = expected. T = theoretical.

Another plant, 1514*a*(1), of similar origin (882(5) × R_1 type) proved to be resistant to all strains and to possess the genes R_1R_2 (Tables XXVI and XXVII). When back-crossed to the female parent (882(5)) the theoretical segregation ratio is $1R_1R_1R_2R_2 : 2R_1R_1R_2 : 1R_1R_1 : 2R_1R_2R_2 : 4R_1R_2 : 2R_1 : 1R_2R_2 : 2R_2 : 1r$. Strain C kills the three R_2 types and the recessive (25 per cent.), strain F kills the three R_1 types (18·75 per cent.), and nine plants (56·25 per cent.) survive. If the sequence of strains is reversed the proportions remain the same, because the recessives succumb to the first strain applied.

The segregations obtained by crossing 882(5) (R_1R_2) with 1104 (R_3R_4) are shown in Table XXVIII. The expected segregation is as follows:—

$1R_1R_2R_3R_4$	$1R_1R_2$	$1R_1$
$1R_1R_2R_3$	$1R_1R_3$	$1R_2$
$1R_1R_2R_4$	$1R_1R_4$	$1R_3$
$1R_1R_3R_4$	$1R_2R_3$	$1R_4$
$1R_2R_3R_4$	$1R_2R_4$	$1r$
	$1R_3R_4$	

Against strain B^2 only genes R_2 and R_3 are effective and a 3 : 1 ratio is obtained. Likewise against strain E only R_2 and R_4 are effective and a 3 : 1 ratio results.

TABLE XXVIII.—PROGENIES DERIVED FROM 882(5) AND 1104

Ref. No.	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1518*d*	882(5) × 1104*a*(3)	B^2	116	37	3·14 : 1	3 : 1	
1519*bc*	do. × do.	E	269	100	2·69 : 1	3 : 1	
1521*c*, 1522*a*	882(5) × 1104*c*(2)	B^2	356	136	2·62 : 1	3 : 1	$R_1R_2 \times R_3R_4$
1921*de*, 1922*bc*	do. × do.	E	626	205	3·05 : 1	3 : 1	
1919*a*	882(5) × 1563*a*(18)	C	91	22	4·14 : 1	3 : 1	$R_1R_2 \times R_3$

In the double test (Table XXIX), where E is followed by C, all plants lacking genes R_2 and R_4 are killed (*i.e.* 25 per cent.) by strain E, and of the remainder those lacking genes R_1 and R_3 are killed by strain C (*i.e.* 18·75 per cent. of the original number). The survivors (56·25 per cent.) are resistant, not only to C and E but also to A, B^1, B^2 and D. In progeny 1919*a*, the pollen parent 1563*a*(18) was bred from Craigs Defiance × 1104*a*(3). The genes involved are R_3 and R_4, but since 1563*a*(18) is itself susceptible to strain E, it must possess gene R_3 only.

TABLE XXIX.—DOUBLE TESTS

Ref. No.	Parentage		Killed by E	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1522*c*	882(5) × 1104*c*(2)	O	53	30	109	192	$R_1R_2 \times R_3R_4$
		E	48	36	108	192	
		T	4	3	9	16	
			C	F			
1919*a*	882(5) × 1563*a*(18)	O	22	41	50	113	$R_1R_2 \times R_3$
		E	28·25	42·375	42·375	113	
		T	2	3	3	8	

O = observed. E = expected. T = theoretical.

882(5) (R_1R_2) crossed with R_3 gives the segregation $1R_1R_2R_3 : 1R_1R_2 : 1R_1R_3 : 1R_2R_3 : 1R_1 : 1R_2 : 1R_3 : 1r$. The C strain kills the R_2 plants and the recessive (25 per cent.), and the F strain kills all the remainder

which lack gene R_2 (37·5 per cent.). The survivors (37·5 per cent.) must possess at least gene R_2 together with either R_1 or R_3. Plants so constituted are resistant to all seven strains of the parasite.

The female parents, 1518*d*(2) and 1521*c*(6), referred to in Table XXX were bred from 882(5) × 1104 ($R_1R_2 \times R_3R_4$), and were survivors of tests

TABLE XXX.—PROGENIES DERIVED FROM SEEDLINGS OF (882(5) × 1104)

Ref. No	Parentage	Strain	Number of Seedlings R	Number of Seedlings r	Ratio Observed	Ratio Theoretical	Genotypes (Significant Terms only)
1956*cd*	1518*d*(2) × 914*b*(52)	A	95	14	6·79 : 1	7 : 1	$R_2R_4 \times R_1$
1957*b*	do. × 1514*a*(1)	C	86	53	1·62 : 1	1 : 1	$R_2R_4 \times R_1R_2$
1957*a*	do. × do.	F	118	39	3·03 : 1	3 : 1	
1958*f*	1521*c*(6) × 23–22	B^2	63	20	3·15 : 1	3 : 1	$R_2R_3R_4 \times r$
1958*a–e*	do. × do.	C	265	369	0·72 : 1	1 : 1	

recorded in Table XXVIII. Seedling 1518*d*(2) proved to be susceptible to strain C and consequently it can possess neither R_1 nor R_3 genes. Since it is resistant to F, however, gene R_2 must be present. The presence also of gene R_4 is revealed by the A strain test of progeny 1956*cd*. The pollen parent of this progeny is an R_1 type, and the segregation ratio of 7 : 1 shows that three genes are in operation, two of which must be supplied by 1518*d*(2). The constitution of 1518*d*(2) is therefore R_2R_4, and when it is crossed with 1514*a*(1) (genotype R_1R_2 as shown in Table XXVI) the theoretical segregation is as follows:—

$1R_1R_2R_2R_4$	$1R_2R_2R_4$
$2R_1R_2R_4$	$2R_2R_4$
$1R_1R_2R_2$	$1R_2R_2$
$2R_1R_2$	$2R_2$
$1R_1R_4$	$1R_4$
$1R_1$	1r

In the double test (Table XXXI) strain F kills the segregates lacking gene R_2 (25 per cent.), and of the remainder strain C kills those lacking gene R_1 (37·5 per cent.). The survivors (37·5 per cent.) have at least R_1 and R_2 in their constitution. When strain C is used first it kills all genotypes lacking R_1 (50 per cent.). Of the remainder, strain F can kill only the R_1R_4 and R_1 types (12·5 per cent.), and the survivors are the same as before (37·5 per cent.).

Seedling 1521*c*(6) was found to be resistant to all strains and must therefore possess gene R_2. In crosses with the recessive pollen parent

23–22 (Table XXX) it gave progenies which segregated in approximately equal proportions in the C strain test, indicating the presence of either R_1 or R_3. The test with strain B^2 confirmed the gene as R_3, because the 3 : 1 segregation is possible only by the combined effect of R_2 and R_3. The presence of gene R_4 may also be assumed in view of the difference between the results of the double tests, C followed by E and C followed

TABLE XXXI.—DOUBLE TESTS

Ref. No.	Parentage		Killed by F	Killed by C	Survived	Total	Genotypes (Significant Terms only)
1957*a*	1518*d*(2) × 1514*a*(1)	O	39	51	67	157	$R_2R_4 \times R_1R_2$
		E	39·25	58·875	58·875	157	
		T	4	6	6	16	
			C	F			
1957*b*	do. × do.	O	53	29	57	139	$R_2R_4 \times R_1R_2$
		E	69·5	17·375	52·125	139	
		T	8	2	6	16	
1958*cde*	1521*c*(6) × 23–22	O	229	66	81	376	$R_2R_3R_4 \times r$
		E	188	94	94	376	
		T	4	2	2	8	
			C	E			
1958*a*	do. × do.	O	77	19	41	137	$R_2R_3R_4 \times r$
		E	68·5	17·125	51·375	137	
		T	4	1	3	8	

O = observed. E = expected. T = theoretical.

by F. Gene R_4 confers resistance to E but not to F, and hence the difference in the proportions observed. Thus the constitution of 1521*c*(6) is represented by $R_2R_3R_4$, and the theoretical segregation, on crossing with a recessive, is as follows: $1R_2R_3R_4 : 1R_2R_3 : 1R_2R_4 : 1R_3R_4 : 1R_2 : 1R_3 : 1R_4 : 1r$. In the double test, strain C kills all plants lacking gene R_3 (50 per cent.), strain F kills the R_3 and R_3R_4 types (25 per cent.), and the $R_2R_3R_4$ and R_2R_3 types survive (25 per cent.). When strain E is employed instead of strain F only the R_3 types are killed (12·5 per cent.), and the $R_2R_3R_4$, R_2R_3 and R_3R_4 types survive (37·5 per cent.).

DISCUSSION

Some twenty years ago Müller (1930) showed that the inheritance of resistance to *Phytophthora infestans* in the potato is complex. The segregations he observed could not be compared strictly with standard Mendelian ratios, and the findings were explained by postulating four allelomorphic genes of different numerical value. Resistance was attained

in a plant only when the sum of these values in its genotype reached a certain numerical level. Later, an investigation was made by Lehmann (1941) in an attempt to assess the potentialities of nine varieties of the species *S. demissum* as a genetic source of resistance. In all crosses between resistant and susceptible forms, the whole F_1 generation was found to be resistant. Further, the segregations in F_2 and in back-cross generations showed that the differences in resistance were conditioned by Mendelian genes. The mode of inheritance was found to be the same for resistance to the two different strains of *Phytophthora* employed, and reciprocal crosses gave identical results. Apparently the lack of a suitable series of *Phytophthora* biotypes or strains prevented the differentiation of genes in these experiments.

The main feature of the present experiments is the identification in the hereditary constitution of *S. demissum* (CPC 2127) of four different major genes each conferring different and distinct reactions to infection with strains of *Phytophthora infestans*. The existence of three of these genes had been previously established (Black, 1950), but it was only with the discovery of a fourth gene that several early results, apparently anomalous, could be fully explained and the range of data fitted to a relatively simple Mendelian scheme. No evidence of the existence of any further major genes in CPC 2127 has come to light. It is of interest that each gene so far identified induces in the plant a hypersensitive response to infection not only with the common strain, but also with a particular group of biotypes. Although only six specialised strains were employed, it is clear that a larger number could be differentiated by the four genes without affecting the genetic principles involved.

The identity of the individual genes could not be fully established in the early generations of the experiments because of the lack of sufficient strains of the parasite and the obscurity of the segregations caused by the presence of more than one gene. In later generations, when the genes had become separated by means of back-crossing to recessives, it became possible to study them individually and to establish that the mode of inheritance was similar in each case and in conformity with Mendelian principles. However, three important deviations from standard disomic ratios were observed. The first occurred in early generations derived from *S. demissum* ($2n=72$) and *S. tuberosum* ($2n=48$) when chromosome numbers were irregular and unpaired chromosomes were frequent. The expected Mendelian ratios were not obtained in this case due to the frequency of inclusion of unpaired chromosomes. Similar irregularities in chromosome behaviour with consequent breeding results have been recorded by Salaman (1928), Becker (1939), Schnell (1948) and others.

The second type of deviation was characterised by a consistent excess of recessive segregates in certain parental combinations, particularly in back-crosses to varieties of *S. tuberosum*. This was found to become less pronounced in later generations, and was ascribed to the action of minor incompatibility factors which tended to be eliminated as the breeding work progressed.

The third type of deviation consisted of a large excess of resistant segregates. In the progenies concerned it was found that the resistant parent possessed two identical genes, presumably carried by two identical *S. demissum* chromosomes. If similar chromosomes of similar origin have a greater affinity for each other than *S. demissum* chromosomes have for their *S. tuberosum* counterparts, then unbalanced ratios amongst segregants would result. Such preferential pairing of chromosomes (*i.e.* partial auto-syndesis) would cause a greater proportion than normal of the available R genes to be distributed in the progeny in the simplex condition, and a correspondingly smaller proportion to be inherited in the duplex state. Such a distribution of R genes would cause an increase in resistant segregates at the expense of recessives. In the experiments, preferential pairing was observed in two cases to reach approximately 50 per cent. Some evidence of the occurrence of auto-syndesis in *S. demissum–S. tuberosum* hybrids has been reported by Schnell (1948).

The fact that one or other of these deviations was in evidence in the majority of the progenies tested, illustrates their significance in the elucidation of the problem and in its practical application. No doubt they are the inevitable consequences of interspecific hybridisation, involving species that are not wholly compatible and have differences in chromosome number.

Having identified the genes and recorded their individual relationships to the different *Phytophthora* biotypes, it is interesting to review the early generations through which the genes had been transmitted. The triple hybrid lines provide evidence for this purpose, since all four genes were found in them. The original cross *S. Rybinii* × *S. demissum* produced one plant, Seedling 735, which, on crossing with three different varieties of *S. tuberosum*, gave rise to seven triple hybrid offspring. These are shown in Table XXXII together with the genes accredited to them. Unfortunately two of the triple hybrids, 884(1) and 885(3), failed to survive long enough to be fully examined. It is unlikely, however, that they contained any new genes, since segregations in progenies bred from 735 indicate the presence of four genes only. The F_1 hybrid (735) may therefore be represented by $R_1R_2R_3R_4$ and *S. demissum* by the same genes in the homozygous condition.

TABLE XXXII.—GENES IDENTIFIED IN *S. demissum*, HYBRID 735 AND THE TRIPLE HYBRID SEEDLINGS

S. demissum (CPC 2127)	$R_1R_1R_2R_2R_3R_3R_4R_4$
735 (*S. Rybinii* × *S. demissum*)	$R_1R_2R_3R_4$
884(1) (735 × *S. tuberosum*)	$R_1R?$
885(1)	R_1
(2)	R_1R_3
(3)	$R_3R?R?$
(4)	$R_1R_3R_4$
886(1)	R_2R_4
(2)	R_1

The distribution of four independent genes in the 72 chromosome species *S. demissum* is not clear. The basic chromosome number in potatoes has long been the subject of controversy, and although widely accepted as 12, universal agreement has still to be reached. If 12 is the true basic number, and *S. demissum* chromosomes consist of 3 diploid sets of 24, one of these sets must have resistance genes in more than one pair of chromosomes. The presence of four R genes in the F_1 and three in triple hybrid plants precludes the postulation of an allelomorphic association of two R genes for the purpose of limiting resistance factors to three pairs of chromosomes.

As stated in an earlier report (1945), the effect of the major genes is not absolute. Their fundamental rôle is to determine the general reaction, resistance or susceptibility, but the phenotypic expression may be modified by unidentified minor factors which control the degree of resistance in the presence of major genes, and the degree of susceptibility in the absence of such genes. The classification of seedlings into two groups, resistant and susceptible, presents no serious difficulty provided the necessary care is taken to maintain the vigour of the plants and to ensure that each is properly inoculated. No evidence has been found which suggests that minor genes alone can induce a hypersensitive condition in the plant or are capable of inhibiting the expression of major genes. According to Petterson (1941), foliage resistance may be divided into nine groups ranging from highly resistant to highly susceptible. Detached leaves under very humid conditions were employed for the test. The various groups observed presumably represent degrees of resistance and degrees of susceptibility resulting from the action of different minor gene complexes in the material. The partial resistance observed in the variety President (Stevenson, Schultz, Akeley and Cash, 1945) is caused by minor genes, since the variety is not hypersensitive and possesses no major genes.

It should be emphasised that the resistance referred to in the present

experiments is foliage resistance, since the reactions of different parts of the plant need not necessarily be identical. Tests of young seedlings revealed that resistant leaves and susceptible cotyledons may occur in the same plant. In such cases the reaction of the cotyledons must be ignored in order to classify accurately a crop plant which is normally vegetatively reproduced. Examination of tubers of the different genotypes showed that, in a general sense, tuber resistance tended to follow leaf resistance although it was usually weaker and less consistent. Different varieties possessing the same R gene showed considerable variation in depth of penetration by the common strain of the fungus, indicating that minor genes exert a significant effect in tuber resistance. In tubers of each of the four genotypes R_1, R_2, R_3 and R_4 it was possible by graft inoculation to obtain a deep penetration of the tissues by each of the seven strains of the parasite. In a few exceptional cases the entire tubers were quickly discoloured by a strain to which the leaves were fully resistant, but sporulation in such cases was sparse or absent. On the other hand, strain F showed a pronounced lack of vigour on tubers of Craigs Royal, a variety of *S. tuberosum*, although it quickly engulfed those of an R_3R_4 resister, *i.e.* resistant to all strains except F. Differences in the speed of reaction of different parts of the plant have been reported by Müller (1950). He found the reaction to be quickest in young sprouts and leaves, slow in the inner parenchyma of stems, and very slow in petals and the parenchyma of tubers. It is probable that the greater variation in tuber resistance is due to the greater influence of minor resistance factors in organs which react relatively slowly. Differences in the reaction of tubers of susceptible varieties which were observed by de Bruyn (1943) may also be ascribed to the effect of minor genes.

Bonde, Stevenson and Clark (1940) found that tuber resistance and leaf resistance occurred together in a high percentage of cases, but suggested that the two characters may not be controlled by the same genetic factors. Some years later, however, Montaldo and Akeley (1946) demonstrated a definite positive correlation between leaf and tuber resistance. A few exceptions occurred, but these were considered too small in number to invalidate the + correlation.

The research work of Müller and his collaborators (*e.g.* Müller, Meyer and Klinkowski, 1939; Müller, 1941; Müller and Boerger, 1941; Müller and Behr, 1949; Müller, 1950 on the physiology of resistance led to the conclusion that resistance genes act as accelerators of a defence reaction which susceptible genotypes are also capable of producing. The genes are nor responsible for the resistant condition itself, but merely induce a genetic predisposition of the tissues to acquire a local immunity from

infection when brought into contact with parabiontic races of the parasite. Thus the reaction speed in resistant genotypes is relatively fast while in susceptibles it is relatively slow. These and other conclusions reached from the physiological aspect provide an understanding of the nature of resistance and of the functions of the genes, without conflicting in any way with the genetic interpretation of the problem.

The instability and adaptability of *Phytophthora infestans* are now universally acknowledged, but the exact mode of origin of specialised races can seldom be specified. The fungus, being aseptate and multinucleate, may become altered in its pathogenicity by means of saltation, and it is probable that some of the quantitative differences in virulence which have been observed may result from such changes. Hybridisation may also provide a means of alteration in infective power, since the formation of oospores has been observed (*e.g.* Clinton, 1911), although only rarely. The infrequency of sexual reproduction, however, suggests that this method is relatively unimportant as an evolutionary process. The most significant changes appear to result from mutation, and the major qualitative differences in pathogenicity may be attributed to it.

Changes in the infective power of *Phytophthora infestans* have been recorded by several investigators. Reddick and Mills (1938) and Reddick (1940) found an increase in virulence after the fungus had completed several passages through varieties which were partly resistant to the original form. This increased virulence remained unreduced even after continuous culture for 20 generations on ordinary susceptible varieties. Reddick considered that the greater virulence could be induced at will by culture on partial resisters, but this opinion was not confirmed in experiments by Bonde, Stevenson and Clark (1940).

Investigations comparable with those of Reddick and Mills were carried out by de Bruyn (1947) using single spore cultures. She found that certain strains which normally parasitised potatoes became adapted to tomatoes after several passages through them, and that the new strains retained their powers of attacking tomatoes after further culture on potatoes. She regarded the fungus as very plastic and adaptable, and attributed changes in pathogenicity either to modification of the fungus or to selection of strains.

The number of strains which have been differentiated by investigators has so far been small, except in Germany where 31 different forms were isolated (Müller, 1950). The differentiation of these strains necessitated the use of tubers as well as a test series of foliage types, indicating that differences between some of the strains was small and identifiable only by minor gene differences as expressed in tubers.

The problem of the classification and nomenclature of strains, while steadily increasing in magnitude, remains unsolved. It seems probable that progress could best be made by the use of a range of differential hosts of known genetic constitution and by relating strains to the major genes from the results of foliage tests. If several isolates should fall within any particular "major gene" class, differentiation may be effected by tuber tests.

The strains employed in the present experiments were found in vigorous condition on the foliage of certain genotypes to which they were apparently well adapted. With minor exceptions they were maintained from year to year on leaves and tubers of these genotypes in order to avoid as far as possible any change in pathogenicity. The exact origin of the strains

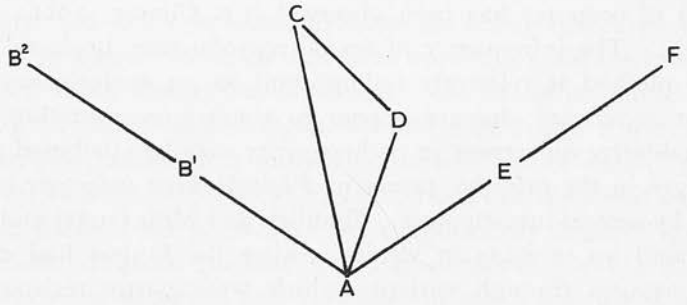

FIG. 6.

cannot be confirmed, but the evidence suggests that their inter-relationships may be as illustrated in fig. 6. Strains B^1, C and D appeared locally in the field plots on genotypes R_1, R_2 and R_4 respectively, while strain E occurred in Tanganyika on seedlings which were undergoing trial in tropical conditions. All are presumed to have arisen from strain A.

Strain B^2 probably arose from B^1, which it unsuspectingly replaced sometime between the 1946 and 1947 seasons. The change was first revealed in 1947 by the character of the segregation ratios of certain progenies (Black, 1949). Further investigations showed that two genes, R_3 and R_4, were present, both of which conferred resistance to strain B^1, while only one of them, R_3, was effective against strain B^2. It is probable that the B^2 strain became established on a segergate with the constitution R_4 and was propagated from that source.

Since strain C occurred in the field in 1944 and strain D three years later, it is probable that they arose independently from the common strain. In an experiment, however, involving the repeated inoculation of an R_2 genotype with strain D, a culture was obtained which proved indistinguishable

from strain C. On that evidence strain C may arise either from D or from the common strain as indicated in fig. 6.

Strain F occurred on a plant which had previously been subjected to a test with strain E and to which it had proved resistant. A single lesion appeared on a leaflet a few weeks after the completion of the E test. The leaflet was detached and the plant reinoculated with E to confirm its resistance. There can be little doubt that F arose from E, since no other strain was in use at the time.

The available evidence on the origin of strains indicates that new forms arise frequently. Sansome (1940) suggested that somatic mutations are of frequent occurrence from generation to generation, and that the process of specialisation could only be considered complete when a new strain appeared which could not survive on the ordinary susceptible commercial varieties. If mutations occur so freely—as they appear to do—the so-called common strain is in fact a population remaining at an equilibrium determined by its environment. Likewise a specialised strain may originate from a single zoospore, but eventually by mutation or other means it will develop into a population provided environmental conditions permit. Success or failure of a new mutant will depend primarily upon the availability of suitable host varieties, and consequently specialisation is directly related to the progress of plant breeding. Other factors, such as climatic conditions, appear to have some influence on the direction of specialisation under natural conditions, just as strains of rust fungi in cereals are associated with particular climatic areas. Given suitable environmental conditions, however, the evidence indicates that any single zoospore isolate has the inherent ability to become eventually a population capable of producing new mutant forms and new populations of different pathogenicity.

The main problem, the breeding of commercial varieties resistant to the fungus, is clearly indicated in the light of the above considerations. By means of repeated back-crossing to commercial varieties the different genes controlling hypersensitivity to the disease in the wild species become isolated from each other, and can be identified by their phenotypic reaction to infection with the various biotypes. No single gene is capable of providing protection against all biotypes, but the combined effect of two, viz. R_1+R_2 or R_2+R_3, was found to be adequate for resistance to the seven strains employed. No doubt further new strains will appear, and it is possible that new forms may arise which are capable of attacking the gene combinations mentioned. Nevertheless, since each gene is inherited independently in dominant fashion and no linkage appears to exist between these genes and genes controlling characters unacceptable in commercial

varieties, it is now possible to direct the recombination of all four resistance genes, *e.g.* $R_1R_2 \times R_3R_4$, and so produce new economic varieties with a level of resistance comparable with that of the original wild species.

Summary

1. The common strain and six specialised strains of *Phytophthora infestans* were employed in testing seedlings and seedling progenies, obtained from four different breeding systems, for resistance to the disease.

2. The resistance exhibited by *S. demissum* (CPC 2127) and seedlings bred from it is due primarily to the hypersensitive condition of the protoplasm. This condition is manifested in the presence of one or more major resistance genes, of which four have been identified, viz. R_1, R_2, R_3 and R_4.

3. Each major gene confers resistance to the common strain and to a particular group of specialised strains of the parasite. The genes are inherited independently in simple Mendelian fashion.

4. A series of minor genes, associated with morphological and physiological characters of the plant, modify the phenotypic expression of the major gene system, and so determine the degree of susceptibility in susceptible phenotypes and the extent of necrosis in resistant ones.

5. In the early generations of *S. demissum–S. tuberosum* hybrids, the irregularity of chromosome behaviour and the presence of unpaired chromosomes caused the ratios of resistants to susceptibles to vary widely from standard Mendelian ratios.

6. In certain progenies, particularly those obtained by crossing *S. tuberosum* plants with resistant hybrid derivatives of *S. demissum*, deviations from standard Mendelian ratios were consistent in their trend, and appeared to be due to some relationship between genes affecting disease resistance and incompatibility genes.

7. In certain parent seedlings with duplicate genes, derived from self-fertilised plants or from recombination crosses, partial auto-syndesis resulted in an excess of resistant segregates in the progenies.

8. The so-called common strain of *Phytophthora infestans* is regarded as a population persisting at an equilibrium determined by host range and environmental conditions.

9. Specialisation may occur in many directions, mainly by mutation, but new forms survive only when the appropriate host plants are available and the environmental conditions suitable. Specialised races are unlikely to be more destructive than the common strain towards commercial varieties of *S. tuberosum*; some are appreciably less virulent.

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